Volume 63 Number 2
July 16, 2009
ISSN 0024-0966

Journal of the Lepidopterists' Society

Published quarterly by The Lepidopterists' Society

THE LEPIDOPTERISTS' SOCIETY

The object of The Lepidopterists' Society, which was formed in May 1947 and formally constituted in December 1950, is "to promote the science of lepidopterology in all its branches, . . . to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

Membership in the Society is open to all persons interested in the study of Lepidoptera. All members receive the *Journal* and the *News of The Lepidopterists' Society*. Prospective members should send to the Assistant Treasurer full dues for the current year, together with their full name, address, and special lepidopterological interests. In alternate years a list of members of the Society is issued, with addresses and special interests.

Active members—annual dues $45.00 within the U.S., $50.00 outside the U.S.
Affiliated members—annual dues $10.00 within the U.S., $15.00 outside the U.S.
Student members—annual dues $20.00 within the U.S., $25.00 outside the U.S.
Sustaining members—annual dues $60.00 within the U.S., $65.00 outside the U.S.
Life members—single sum $1,800.00
Institutional subscriptions—annual $60.00, $65.00 outside the U.S.
Airmail postage for the *News* $15.00, $30.00 outside North America (U.S., Canada, Mexico)

Send remittances, payable to *The Lepidopterists' Society*, to: Kelly M. Richers, Treasurer, 9417 Carvalho Court, Bakersfield, CA 93311; and address changes to: Julian P. Donahue, Natural History Museum, 900 Exposition Blvd., Los Angeles, CA 90007-4057. For information about the Society, contact: Ernest H. Williams, Department of Biology, Hamilton College, Clinton, NY 13323. To order back issues of the *Memoirs*, write for availability and prices to Kenneth R. Bliss, 28 DuPont Avenue, Piscataway, NJ 08854.

The additional cost for members outside the U.S. is to cover mailing costs.

Journal of The Lepidopterists' Society (ISSN 0024-0966) is published quarterly by The Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, CA 90007-4057. Periodicals postage paid at Los Angeles, CA and at additional mailing offices. POSTMASTER: Send address changes to The Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, CA 90007-4057.

Cover Illustration: Female *Lycaena xanthoides* feeding on Willamette Valley gum weed extrafloral resin on the unopened capitulum. Photograph by Paul Severns. See journal article on page 83.

Journal of The Lepidopterists' Society

Volume 63 2009 Number 2

Journal of the Lepidopterists' Society
63(2), 2009, 61–82

THE RIODINID BUTTERFLIES OF VIETNAM (LEPIDOPTERA)

Curtis J. Callaghan

Calle 93 5-45 Apt.302, Bogotá, Colombia; email: curtiscallaghan@yahoo.com

ABSTRACT. A review of the 29 riodinid taxa found in Vietnam is presented, including notes on taxonomy, diagnosis, behavior, habitat and range. The following nomenclatural changes are made: *Dodona eugenes maculosa* is returned to its original designation, *Dodona maculosa* Leech,1890 **reinst. stat.**; *Dodona deodata longicaudata* is returned to species status as *Dodona longicaudata* Niceville, 1881 **reinst. stat.**, and *Dodona deodata lecerfi* is raised to species status as *Dodona lecerfi* Fruhstorfer, 1914, **n.stat.** *Abisara echerias notha* Bennett 1960 is synononomized with *A. e. paionea* Fruhstorfer, 1914, **n. syn**.; *Abisara geza latifasciata* Inuoé & Kawazoé, 1965, is raised to species status as *A. latifasciata* **n. stat**; *Abisara savitri attenuata* (Tytler, 1915), is returned to species status as *Abisara attenuata* **reinst. stat.**, *Taxila dora hainana* Riley & Godfrey, 1925, is raised to species status as *Taxila hainana* **n. stat.**; *Stiboges nymphidia elodinia* Fruhstorfer 1914, is raised to species status as *Stiboges elodinia* **n. stat.**. The genitalia and facies of complex taxa are illustrated as explanations for the nomenclatural changes. Data on the biogeography of each taxon in Vietnam are presented, and compared with distributions in Indo-China.

Additional key words: : Indo-Malayan Realm, Indochina, Laos, Cambodia, Thailand, biogeography, biology, habitats, behavior, genitalia

The riodinid butterflies of Vietnam are poorly known. Despite a long period of French colonial administration, few Europeans took an interest in the butterfly fauna. Also, much of the 20th century was taken up by armed conflicts, which prevented much serious collecting.

Most early records come from Fruhstorfer, who, during the last decade of the 19th century, collected in "Tonkin", today known as North Vietnam. He was followed in the 1950s by Roger Métaye (1957), whose efforts regarding riodinids were minimal. In the early 1960s, the Japanese scientists, Inuoé and Kawazoé collected only briefly in South Vietnam. The result is a dearth of material and records in major museums, not only from Vietnam, but from Laos and Cambodia as well. The Vietnamese specimens in the Natural History Museum, London are few beyond those collected by Fruhstorfer, and a handful of additional specimens from the colonial period are at the Muséum National d'Histoire Naturelle, Paris.

This situation started to change with agreements between the Vietnamese Government and foreign organizations for the purpose of documenting the biodiversity of the country. With increased investigation, Vietnam is becoming known as an extremely complex region with many endemic taxa of birds, butterflies and mammals. This study recognizes 27 species of riodinids, of which 3, or 10% are endemic. For Thailand, a much larger country, Pinratana (1988) records 29 and Corbet & Pendlebury (1992) list 16 species for Malaysia.

Materials and Methods

This revision was based on specimens from a number of different sources. I studied type specimens and the collections at the Zoologisches Museum für Natürkunde, Humboldt-Universität, Berlin, Germany (ZMHU), the Muséum National d'Histoire Naturelle in Paris (MNHN), and the Natural History Museum, London (BMNH). Additional types are in the Moscow State University (MSU). Private collections studied were those of the author and Alexander Monastryrskii of the Vietnam Russian Tropical Centre in Hanoi. A total of 341 Vietnamese specimens were examined, as well as others from neighboring countries including 19 primary types. Ninety-five genitalia preparations were made. Dissected and voucher specimens are in the collections of the author (CJC) and A. Monastyrskii (ALM), and the MNHN.

Biogeography. Vietnam forms part of the Indo-Malayan Realm, sometimes referred to as the Oriental Region. This extends from western Pakistan eastwards south of the Himalayan Mountains through southern China to the island of Taiwan, then south to include

India, Indo-China, the greater Sunda islands and the Philippines to the variously-defined western border of the Papuo-Australasian Realm. Geographically, the Indo-Malayan Realm can be divided into three regions; the Indian sub-continent, Indochinese region and the Malay archipelago, or Sundaland.

Indo-China, to which Vietnam belongs, was part of Laurasia, which separated from northern Gondwanaland about 120 million years ago. Indo-China can be divided into three regions. In the west, the Chin and Patkai hills form a barrier with India. This gives rise to four great south flowing rivers that follow divergent courses, the Salween, Mekong, Red and Black rivers. They form basins divided by ranges of low hills before emptying into broad alluvial plains and the Gulfs of Thailand and Tonkin.

The largest of these basins is the Mekong and Chao Phraya valleys of present day Laos and Cambodia, which form the second geographical subdivision between the Tanen Tong hills and the Annamite mountain chain on the Vietnam-Lao border. The final southeast Asian division is the drainage to the Gulf of Tonkin east of the Annamites and north to the Red River delta in present day Vietnam, the southern coastal plains of China and the islands of Hainan and Taiwan.

These three regions also reflect diverse climatic conditions. The Chin and Patkai hills region in Burma starts with the high rainfall of the Himalayan plateau, decreasing to 1000–2000mm/yr in the east through the Mekong basin to the Annamites, and then increasing to 2000–3000mm/yr along the Vietnamese coastal plain north to coastal China and Taiwan island. Throughout these regions climate and rainfall vary considerably depending on topography, latitude and altitude. The pattern of rainfall in Vietnam is typical of the rest of tropical Asia with two monsoon seasons. A relatively dry period occurs during the northern winter months (November to April) following a wet period with heavy rains during the northern summer (May to October).

The fauna of the Indo-Malayan Realm is derived mostly from the Palaearctic and Afro-tropical biotas. There are few endemic families of animals as compared to the Neotropical or Afro-tropical Realms due to its relatively recent origin. However, because the Realm is geologically very active with land connections coming and going, and with a relatively stable tropical climate, the conditions are created for high levels of local endemism on the specific and generic levels.

The fauna of the Indo-Chinese sub-region shows richness comparable to other parts of the Realm, but considerably lower endemism. The fauna is a mixture of Palaearctic and south China species. Some Malaysian species enter into the southeast coast of southern Vietnam. In North Vietnam, the Red River and delta form an effective barrier to the dispersion of many species.

Vietnam has a number of prominent geographic features. North of the Red River the land rises towards the Chinese border and is punctuated by a number of limestone mountains comprising the Indochina limestone karst. South of the Red River along the Chinese border are the Hoarglier Mountains that rise to 3000m at Mt Farsipan, the highest point in Indochina. To the southeast are the highlands of the Xiarg Khouang Plateau on the Laotian border. The highlands terminate in a series of rugged limestone hills. To the south the central Vietnam coastal plain is bordered on the west by the Annamite mountain range following the Laotian border. The Annamite range is divided into three main sections. The northern Annamites extend from Nghe An province south to Quang Binh Province. The narrow coastal plain is hot and humid, drenched by the Northeast monsoon. The central Annamites are more extensive and nearly reach the sea between Quang Tri and Gia Lai Provinces, and extend into Laos. The southern Annamite Mountains, or the Dalat Plateau, is nearly entirely within Vietnam and forms a high plateau reaching to 1500m between Gia Lai and Lam Dong Provinces. The coastal plain here is very dry, lying in the rain shadow of the mountains. To the south the land drops into the alluvium plains around the Mekong delta.

The distribution of the Riodinidae in Vietnam is also influenced by the geography of the country. The Annamite range with altitudes to over 2000m allows temperate climate species to inhabit Central and South Vietnam. Primary among these is the genus *Dodona* (Fig.61). These same features allow a similar distribution of temperate middle altitude *Paralaxita*, *Taxila* and *Abisara neophron* group species over the same range (Figs. 63, 64). The range of the lowland tropical *Abisara echerias* group (Fig. 62), however, shows a sharp division along the Red River of North Vietnam, suggesting that this has been an effective barrier to dispersion.

Localities and habitats. In the study of the Vietnam fauna, 17 areas were sampled for riodinids. Three additional sites were located from material examined. These localities are described below, from north to south. An additional 14 Indochina localities were taken from the literature. The locations are shown on the map, Figure 1.

North Vietnam – Tonkin

1. Hoang Lien Nature Reserve, Sa Pa District, Lao Cai Province, 22°09'–24°00'N 103°47'–59'E. The reserve is in the Hoarg Lien Mountains on the Chinese

border south of the Red River valley and near the town of Sa Pa. The forest is montane dry evergreen, tropical montane deciduous, and sub alpine forest from 1500 to 3143m on Farsipan peak. The topography is steep, with mountainsides cut by numerous streams. Much of the fauna is Sino-Himalayan. Riodinids range between 1220 and 2150m above sea level (asl).

2. Muong Nhe Nature Reserve, Lai Chau Province, 21°50'–85'N 102°10'–58'E. This reserve is on the Laotian border to the west of the former locality, is dryer and lower, around 300 to 1800m. Habitat is lower montane evergreen forest to 800m and upper montane evergreen forest to 1800m and has been significantly altered by human activity. The principal vegetation formation is secondary scrub and grass savanna.

3. Chiem Hoa, Tuyen Quang Province, 21°14'N 105°33'E. Vegetation is lowland evergreen forest on limestone. Mount Mauson, referred to by Fruhstorfer, is located here.

4. Tam Dao National Park, Vinh Phuc Province, 21°21'-42'N 105°23'-44'E. Once a French hill station, Tam Dao is an isolated mountain peak, reaching 1400m and lying north of the Red River valley and Hanoi. The lower slopes to 800m are altered low montane evergreen forest, but the areas above 900m support good low montane forest formations. Riodinid records are from above 900m.

5. Bai Tu Long Islands National Park, Hai Phong Province. This area is off the coast of North Vietnam and north of the Red River delta. The altitude is sea level to 90m. Disturbed limestone forest is the predominant formation.

6. Cat Ba Island, Cat Ba National Park, Hai Phong Province. 20°44'–51'N 106°45'–85'E. This reserve lies to the south of Bai Tu Long, off the Red River delta. Altitude is sea level to 330m. Vegetation is limestone tropical evergreen forest. Riodinid records are from 100m.

7. Cuc Phuong National Park, Ninh Binh, Hoa Binh, Than Hoa Provinces. 20°14'–24'N 105°29'–44'E. The Park area is characterized by rugged limestone karst hills covered with evergreen forest, from 100 to 636m. The area sampled was between 300 and 550m.

Central Vietnam – Annam

8. Pu Mat Nature Reserve, Nghe An Province, 18°50'–19°00'N 104°20'–55'E. This area extends along the northern Annamite mountain ridge. The terrain is steep and mountainous reaching 2700m. Vegetation is lowland evergreen forest and some deciduous and conifers above 1800m. The higher peaks have cloud forest. The area sampled was between 650 and 1000m.

9. Vu Quang Nature Reserve, Ha Tinh Province, 18°09'–25'N 105°16'–12'E, 300–1600m. This area is the second locality on the northern Annamite ridge and is very precipitous with steep valleys and swift flowing streams. Vegetation is lowland evergreen to lower montane evergreen forest to 1000m, and medium montane forest to 1600m.

10. Ba Na Nature Reserve, Da Nang Province, 15°57'–16°08'N 107°49'–50'E. This area is in the Central Annamite range and is principally lowland evergreen Forest habitat 245–880m with lower montane evergreen forest above. Area sampled was between 200 and 1100m.

11. Ngoc Linh Nature Reserve, Kon Tum Province, 14°45'–15°15'N 107°21'–108°20'E, 1250–1850m. This reserve is also located in the Central Annamite Mountains. Vegetation formations are low montane broadleaf evergreen forest with some medium to high montane evergreen forest. The highest point is Mt. Ngoc Linh (2598m). The area sampled was between 1200 and 1700m.

12. Kon Ka Kinh Nature Reserve, Gia Lai Province, 14°09'N 108°16'E, 1000–1700m. This is a key area of the Central Annamite Mountains. It is assumed to be a climatic gradient to the Northern Annamites. Forest is montane and lower montane broad leafed evergreen and coniferous forest. The terrain is rugged with peaks reaching to 1742m. The area sampled was from 1000 to 1200m.

13. Kon Cha Rang Nature Reserve, Gia Lai Province, 14°26'–35'N 108°30–39'E, 850–1500m. This is the third Central Annamite locality. The vegetation is lower montane and montane evergreen forest. The area sampled was from 850 to 1300m.

South Vietnam - Cochinchin

14. Hon Ba Provincial Nature Reserve, Khanh Hoa Province, 12°02'–15'N 108°57'–109°05'E. This area consists of the Deo Ca Spur, a ridge of high ground forming the extension of the southern Annamites towards the coast. Peaks along the ridge reach 2000m. Habitats are evergreen forest to 1000m and montane evergreen forest to 1700m. The area sampled was between 700 and 1400m.

15. Bao Lam District, Lam Dong Province, 11°38'–52'N 107°42'–50'E. This area is in the southernmost extension of the Southern Annamite chain. The main forest types are low montane, evergreen and secondary forest. Most forest exists above 1500m.

16. Da Lat, km 8, Chutes, Lam Dong Province, 11°47'–20'N 108°20'–40'E.

The capital of Lam Dong Province, Da Lat, was a French hill station. Much material from here was

collected during the colonial period. Habitats are natural coniferous forest (Pinus kasiya).

17. Cat Tien National Park, Dong Nai Province, 11°21'–48'N 107°10'–34'E, to 650m. This area comprises the central and main parts of the southern Annamite massive. The climate of this area is more complex than the northern or central Annamites, rainfall depending largely on orientation, reaching 2850mm in the higher elevations. The vegetation is evergreen and low evergreen forest.

Other Vietnamese localities identified from material examined, but not collected recently:

18. Chau Doc, An Giang Province.
19. Mont du Haute Song Chai, Lao Cai Province.
20. Than-Moi, Lang Son Province.

Indo-Chinese localities from the literature:

Laos
21. Phongsak
22. Boun Neua
23. Oudomsay
24. Xam Neua
25. Xaignabouri
26. Vang Vieng
27. Vietiane
28. Lak Sao
29. Thakhek
30. Thateng

Thailand
31. Nakhon Ratchasima
32. Nakhon Nayak
33. Chonburi
34. Chanthaburi

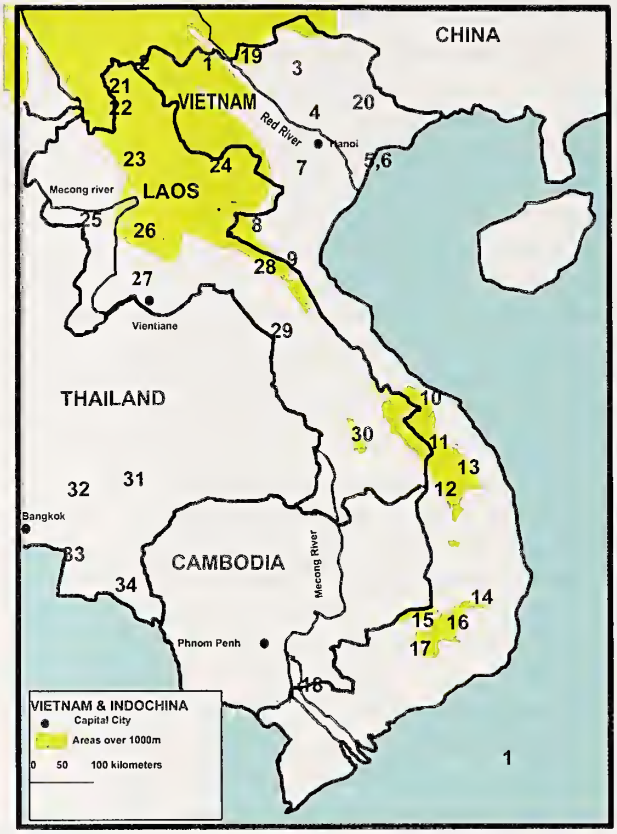


FIG. 1. Map of Indo-China, with numbers of localities given in the text.

A Synonymic List of Vietnam Riodinidae

ZEMEROS Boisduval, 1836

flegyas (Cramer, [1780]) (*Papilio*)
=*annamensis* Fruhstorfer,1912
=*esla* Fruhstorfer,1912

DODONA Hewitson, [1861]

katerina Monastyrskii & Devyatkin, 2000
a.sombra Monastyrskii & Devyatkin, 2003
onida palaya Fruhstorfer, 1914
adonira Hewitson, 1866
egeon (Westwood, 1851) (Taxila)
maculosa phuongi Monastyrskii & Devyatkin, 2000
speciosa Monastyrskii & Devyatkin, 2000
deodata Hewitson, 1876
longicaudata Nieeville, 1881, **reinst.stat.**
lecerfi Fruhsorfer, 1914, **n. stat.**

ABISARA C & R Felder, 1860

=*oenabarus* Toxopeus, 1926, *nom. nud.*

echerias (Stoll, 1790) (*Papilio*)
=*tonkinianus* Fruhstorfer, 1904
a) *paionea* Fruhstorfer, 1914
= *notha* Bennett, 1950, **n. syn.**
saturata meta Fruhstorfer, 1904
=*siamensis* Fruhstorfer, 1904
=*annamitica* Fruhstorfer, 1904
bifasciata angustilineata Inuoé & Kawazoé, 1965
abnormis Moore, 1884
latifasciata Inuoé & Kawazoé, 1965, **n. stat.**
kausambi C & R. Felder, 1860
neophron chelina Fruhstorfer, 1904
=*neophronides* Fruhstorfer, 1914
=*f. gratius* Fruhstorfer, 1912
attenuata (Tytler, 1915) (Taxila), **reinst. stat.**
burnii timaeus (Fruhstorfer, 1904) (*Taxila*)
fylla magdala (Fruhstorfer, 1904) (*Sospita*)
freda Bennett, 1957

***TAXILA* Doubleday, 1847**

dora Fruhstorfer, 1904
hainana Riley & Godfrey, 1925, **n. stat.**

***PARALAXITA* Eliot, 1978**

telesia boulleti (Fruhstorfer, 1914) (*Laxita*)

***LAXITA* Butler, 1879**

thuisto thuisto Hewitson, [1861] (*Taxila*)

***STIBOGES* Butler, 1876**

nymphidia Butler, 1876
elodinia Fruhstorfer, 1914, **n. stat.**

Species Accounts

Genus ***Zemeros*** Boisduval, 1836
Zemeros flegyas flegyas (Cramer, [1780])
(Figs. 2, 3)

=*annamensis* Fruhstorfer, 1912
=*esla* Fruhstorfer, 1912

Papilio flegyas flegyas Cramer, 1780, De Uitlandische Kapellen, v.3, p.158, pl. 175.

The types of *annamensis* and *esla* are in the BMNH.

Diagnosis. Male (Fig 2). Dark brown with both wings covered by arrow shaped black spots bordered distad in white. Female (Fig.3). Same pattern as male but with more rounded wingtips.

Discussion. *Zemeros flegyas* is a variable species found commonly over most of the Indo–Malaysian realm. Twelve subspecies have been described, mainly from the Sunda Islands.

Material from Vietnam shows considerable variation depending on the season and locality. Two forms have been described. *Zemeros annamensis* Fruhstorfer, 1912 —"Darker chocolate brown than males from Tonkin (*flegyas*) which are nearly identical to males from south China, smaller white spots and VS light golden brown. In December, and rainy season", and *esla* Fruhstorfer, 1912 – "small with a broad white apical band. Found in the south in Feb to 1000m." It is similar to subspecies *confucius* Moore, 1878 from Hainan, and *allica* (Fabricius, 1787) from Thailand, but with the sub-apical spot larger and maculation less prominent. In examining specimens from all over Vietnam, I have not been able to associate the two forms with any geographical area, but there appears to be some correlation with season, *esla* more common in the dry season from November to March, and *annamensis* in the wet season from March to October.

Habitat and biology. The flight period is throughout the year, and from sea level to 1600m. This species can be quite common in secondary to severely degraded forest habitats, where they feed on flower nectar during the morning hours. Both sexes will congregate in groups during the middle of the day along trails or clearings. The flight is rapid, but of short duration after which they come to rest on the dorsal surface of leaves not more than a meter off the ground with the wings raised at an angle. The larva has been found in Nepal on *Maesa* sp, (Myrsinaceae), (pers. obs).

Range. The nominate subspecies is distributed from Nepal to Burma, Thailand, Indo-China, and southern China. In Vietnam, *Z. flegyas* is found throughout the country from sea level to 2000m.

Material examined. North Vietnam: 2♂♂ 3♀♀ Hang Lien Song Nat. Reserve, Lao Cai Prov. (ALM); 14♂♂ 1♀ Cuc Phuong, Ninh Binh Prov., 300m (CJC); 6♂♂ 1♀ Tam Dao National Park, Pho Tho Prov. (CJC); 1♂ Bai Tu Long National Park, Islands, (ALM); 1♂ Ba Vi National Park, Ha Tay Prov. (ALM); 1♂ Nam Cat Tien National Park, Phan Quoc Tuan Prov.; 3♂♂ Muong Nhe Nature Reserve, Lai Chau Prov. (ALM); 1♂ 1♀ Cat Ba Island, Hai Phong Prov. (ALM). **Central Vietnam:** 1♂ Kon Ka Kinh Nature Reserve, Gia Lai Prov. (ALM); 1♂ 2♀♀ Kon Cha Rang Nature Reserve, Gia Lai Prov. (ALM); 1♀ Vu Quang Nature Reserve, Ha Tinh Prov. (ALM); 8♂♂ Pu Mat Nature Reserve, Nghe An Prov. (ALM); 1♂ Quang Nam Prov. (ALM); 1♂ Ngoc Linh Nature Reserve, Kon Tum Prov. (ALM). **South Vietnam:** 1♂ Nha Trang Provincial Nature Reserve, Khan Hoa Prov. (ALM); 2♂♂ Bar Dam District, Lam Dong Prov. (ALM).

Genus ***Dodona*** Hewitson, 1867

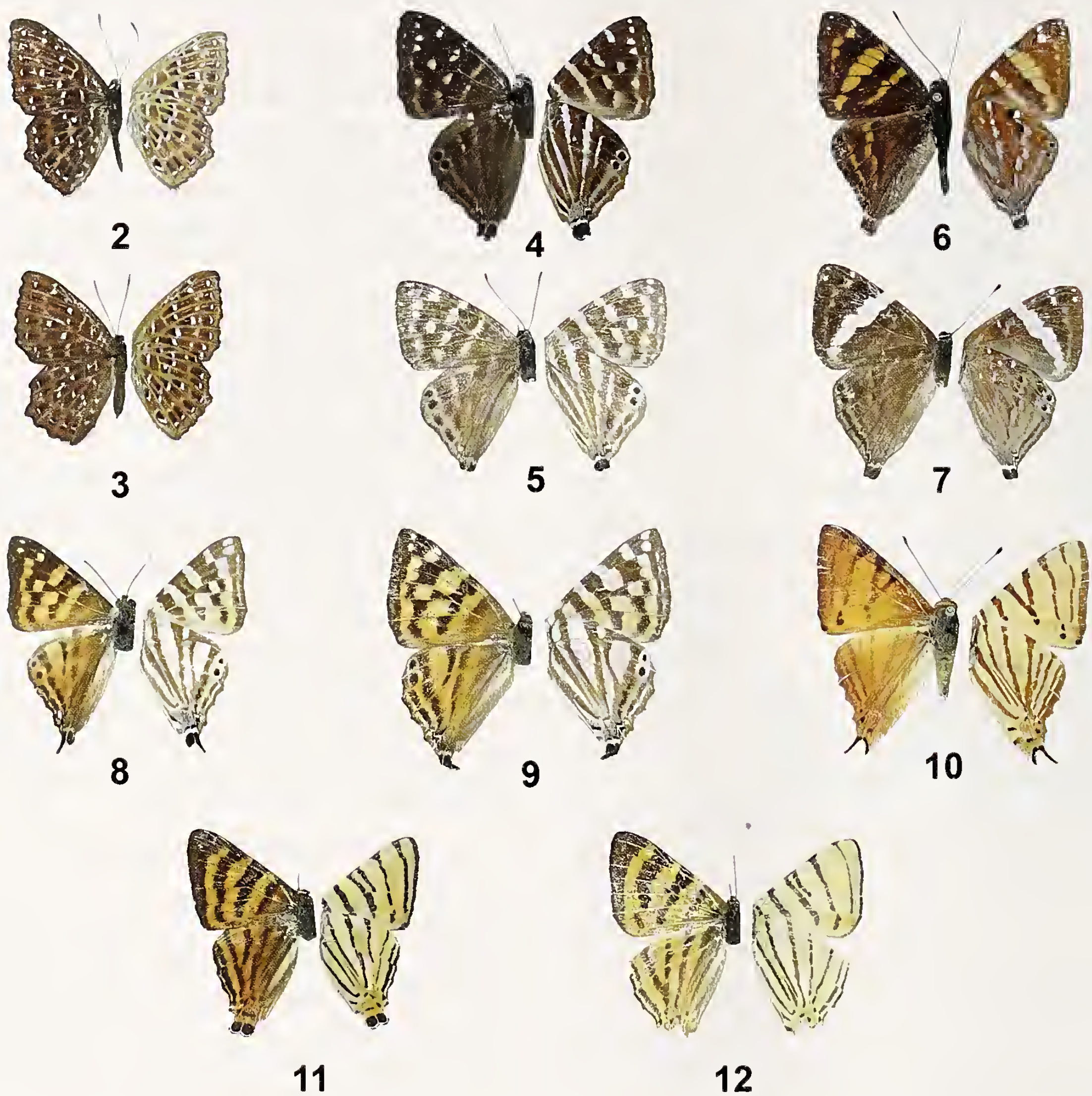
Medium sized butterflies with the forewing triangular, hindwing narrowing to a lobed point at the anal angle or an extended, narrow tail. Stichel (1928) divided *Dodona* into two groups, the Durgiformes without tails and the Egeonformes, with tails. The larvae feed on the genus Maesa (Callaghan, 1997). The adults fly swiftly, resting with wings open or closed. The males are often found on wet sand along streams. Males of some species are strong hilltoppers.

Dodona katerina katerina Monastyrskii & Devyatkin, 2000
Figs. 4, 5, 61

D. katerina, Monastyrskii & Devyatkin, 2000, The zoological Miscellany, (1):[1] tp., 32. (*Papilio*) (Pl.21a figs 1, 2).

This interesting species was described from 2 males and 2 females captured in the Kon Ka Kinh Nature Reserve, 1500m to 1600m, Gia Lai Province in Central Vietnam. The holotype resides in the Moscow State University (MSU). Paratypes are in the BMNH, London.

Diagnosis. Male (Fig.4). Dorsal ground color brown with spots infused with orange scaling. Ventral surface forewing with white spots, hind wing with white lines converging on the anal angle where there is a black bi-lobed extension. Female (Fig.5). Dorsal ground color



FIGS. 2–12. All figures are Vietnamese specimens, except where indicated. **2.** *Zemeros flegyas* male, **3.** *Zemeros flegyas* female, **4.** *Dodona katerina* male, **5.** *Dodona katerina* female, **6.** *Dodona ouida palaya* male, **7.** *Dodona ouida palaya* female, **8.** *Dodona egeon* male, **9.** *Dodona egeon* female, **10.** *Dodona speciosa* male, **11.** *Dodona adonira* male, **12.** *Dodona adonira* female.

light brown with white spots on the forewing. Ventral surface nearly identical to male, but with lighter ground color.

Discussion. The species resembles *Dodona eugenes* without tails. It appears closest to *D. dipoea* and *D. dracon* Niceville, 1897, which likewise have the same bi-lobed anal angle and basic wing pattern. However, *D. katerina* differs in having larger spots and darker brown color on the dorsal surface, broad white bands on the ventral surface, and a white spot on the costa of the hind wing.

In 2003, the same authors described a subspecies *sombra* from a male specimen captured at the Vu Quang Nature Reserve, Ha Tinh Province, 1500m. It differs from the nominate subspecies in its darker ground color. Whether this is an aberrant individual or a geographical race will have to await the examination of additional material.

Comparison of genitalic dissections with figures published with the original description leaves no doubt that the material examined from both North and Central Vietnam represent the same species. A female specimen is figured on Plate 103 in Osada *et al.* (1999) under "*dipoea*" from Xam Neua, Laos, near the Vietnam border. This suggests that the species is much more widely distributed than previously thought.

It is noted that Osada *et al.* (1999) illustrate *Dodona dracon* (as *dipoea*) also from Xam Neua, suggesting that

this taxon is likely to be found in Vietnam.

Habitat and biology. The species inhabits the middle to high montane broad-leafed evergreen forest at about 1500m. Dates: March, April, September; Rare.

Range (Fig.61). From the Chinese border south of the Red River down the Annamite chain to Central Vietnam and eastern Laos.

Material examined. North Vietnam: 3♂♂ Huang Lien Son Nature Reserve (ALM); 1♂ 1♀ Nha Trang, Khanh Hoa Prov. (ALM). **Central Vietnam:** 1♂ 1♀ Kon Ka Kinh Nature Reserve, Gia Lai Prov., 1500–1600m (ALM); 1♂ Vu Quang Nature Reserve, Ha Tinh Prov., 1500m (ALM) (*D. k. sombra*).

Dodona ouida palaya Fruhstorfer, 1914
Fig. 6, 7, 61

Dodona ouida palaya Fruhstorfer, 1914, in Seitz, ed. Grossschmetterlinge der erde, v9. p.777.

Fruhstorfer described the subspecies *D. o. palaya* from "Omeishan" and Mupin in Sze-Tschuan, China. I was unable to locate the type specimen.

Diagnosis. Male (Fig.6). Ground color dark reddish brown, both wings crossed by three yellow orange bands. Ground color on the underside is reddish brown. Hindwing with elongated extension of the tornus, terminating in two black lobes. Female (Fig.7). The forewing is crossed by a broad white irregular band.

Discussion. According to Fruhstorfer, *palaya* from China differs from the nominate subspecies in having a "wider reddish-gold median band on the forewing". He remarks that Karen Hills (Burma) material is a transition to typical *ouida* from Nepal and India. The taxon was not illustrated. Examination of material at the BMNH suggests that the main difference is a darker color in *palaya*, particularly on the ventral surface, which is also typical of Vietnamese material.

Habitat and biology. *D. ouida* perches frequently on hilltops during the afternoon where males can be abundant at times. During the morning hours it can be found absorbing salts by streams with other *Dodona* species (Callaghan 1997). Dates: March, June, September, December. The food plant is *Maesa chisia* Buch. (Myrsinaceae) (Sevastopoulo 1946).

Range (Fig. 61). The species is found in the mountains above 800m from Nepal following the Himalayas across Burma, northern Thailand to southwest China and Indo-China. There is one subspecies from Nepal (*phlegra* Fruhstorfer, 1882). Subspecies *palaya* inhabits southwestern China to east Indochina, and north and central Vietnam.

Material examined. North Vietnam: 10♂♂ 1♀ Huang Lien Son Nature Reserve, Lao Cai Prov., 2000m (ALM); 1♂ Tam Dao National Park, Vinh Phuc Prov., 1300m (CJC). **Central Vietnam:** 2♂♂ Kon Ka Khin Nature Reserve, Gia Lai Prov. (ALM); 2♂♂ Ngoc Linh Nature Reserve, Kon Tum Prov., 1600m (ALM); 4♂♂ 6♀♀ Vu Quang Nature Reserve, Ha Tinh Prov., 1500m (ALM); 1♂ 1♀ Kon Cha Rang Nature Reserve, Gia Lai Prov., 1000m (ALM).

Dodona adonira, Hewitson, 1866
Fig. 11, 12, 61

Dodona. adonira Hewitson, 1865, Exot Butts v4(2) Erycinidae *Dodona* and *Sospita* I, fig. 1,2.

Hewitson described *Dodona adonira* from a male originating from Darjeeling, India, currently in the BMNH. Two additional males are identified as paratypes.

Diagnosis. Male (Fig.11). Ground color dorsal surface dark brown with 4 yellow-orange bands on the forewing and 5 on the hindwing converging on the anal angle, with a black bilobed extension. Ventral surface light yellow with black narrow transverse lines reflecting the dorsal surface interspaced with variable silver scaling on the hindwing. Female (Fig.12). Like male with wider wings and lighter, paler color.

Discussion. Fruhstorfer (1904) described subspecies *argentea* from a northern Burmese specimen with wide borders and faint silver markings between the ventral hindwing veins. Comparison of the Fruhstorfer type (also in the BMNH) with Vietnamese material suggests that the latter are closer to typical *adonira* with wider yellow submarginal bands on both wings. Both have variable silver markings on the ventral hindwing.

Habitat and biology. *D. adonira* inhabits the higher mountains above 1200m. It can be found along streams where it rests with wings open, taking salts and other nutrients. Dates: November, February. Rare in Vietnam. The food plant is *Maesa chisia* Buch. (Myrsinaceae) (Sevastopoulo 1946).

Range (Fig.61). *D. adonira* is found from Nepal to North and Central Vietnam.

Material examined. North Vietnam: 3♂♂ 1♀ Huang Lien Son Nature Reserve, Sa Pa, Lao Cai Prov., 1650m (ALM). **Central Vietnam:** 1♂ Ngoc Linh Nature Reserve, Kon Tum Prov., 1800m (ALM).

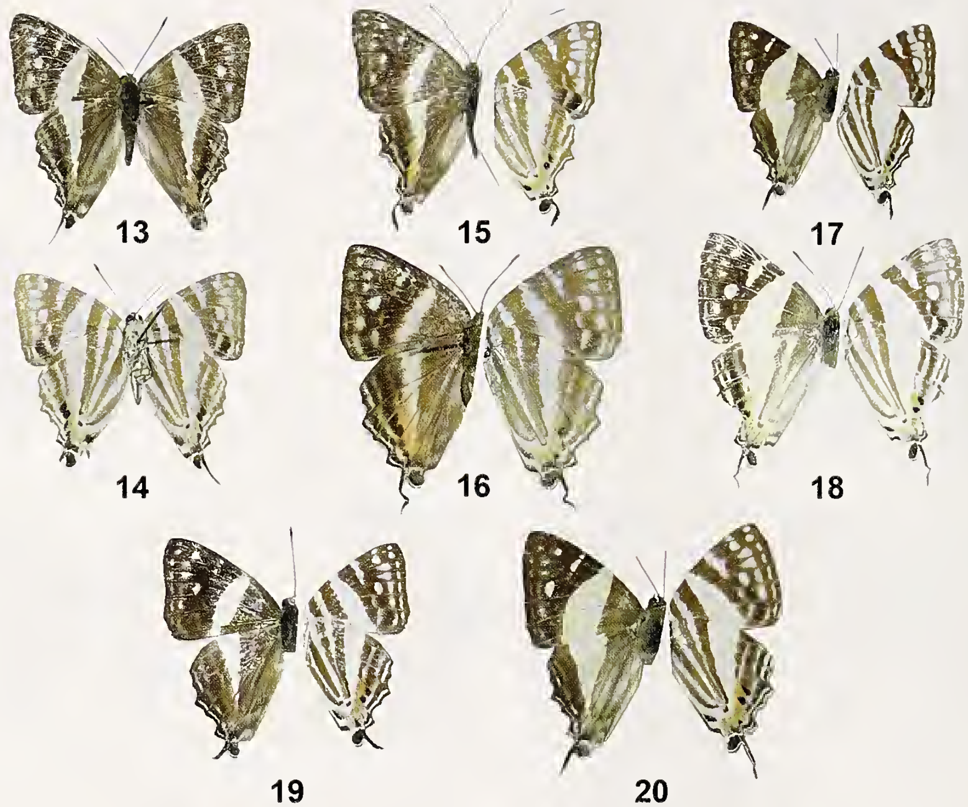
Dodona egeon (Westwood, 1851)
Figs. 8, 9, 61

=*Emesis egeon* Doubleday, 1847, nom. nud.

Taxila egeon Westwood, 1851, in Gen.dium.Lep. 2:422 Pl.69, fig.2.

This species was described from Kumaon, Nepal. It was not possible to locate the type in the BMNH even after an extensive search However, a neotype would not be required even if the type is lost, as the species is well known and common throughout its range.

Diagnosis. Male (Fig.8). Ground color is uniform orange-yellow with irregular checkered black bands



FIGS. 13–20. **13, 14.** *Dodona lecerfi*, holotype, dorsal and ventral, **15.** *Dodona lecerfi*, male form with yellow infusion on hindwing, **16.** *Dodona lecerfi* female, with yellow infusion on hindwing, **17.** *Dodona deodata* male, Thailand, **18.** *Dodona deodata* female, **19.** *Dodona longicaudata* male, **20.** *Dodona longicaudata* female, Andaman Isles.

crossing both wings, converging in two black lobes at the anal angle, the outer of which is extended into a short tail. The ventral surface reflects the dorsal maculation with wide, silver bands on the hind wings. Female (Fig.9). Similar to the male; differs in having wider wings and lighter coloration.

Discussion. The species can be easily separated from other tailed *Dodona* by the dominant orange yellow color of the dorsal surface and the wide bands. Comparison of Vietnamese material with specimens from Nepal shows no significant difference.

Habitat and biology. Vietnam specimens were recorded from disturbed forest at 1500m. During the morning hours, they frequent streams and damp earth. In Nepal, the food plant is *Maesa capitellata* Wall., (1824), (Callaghan 1997). Dates: March. Rare.

Range (Fig.61). *D. egeon* is distributed from Nepal to Vietnam and Laos in the mountains.

Material examined. Central Vietnam: 2♂♂ 1♀ Vu Quang Nature Reserve, Ha Tinh Prov., 1500m (ALM). **South Vietnam:** 1♂ 2♀♀ Nha Trang, Kanh Hoa Prov. (ALM).

Dodona speciosa Monastyrskii & Devyatkin, 2000
Figs. 10, 61.

D. speciosa Monastyrskii & Devyatkin, 2000 The Zoological Miscellany, (1):[1] tp., 32. (Papilio), (Pl.20 figs. 7,8).

This species was described from a single male from Central Vietnam. The holotype is in the MSU.

Diagnosis. Male (Fig.10). Dorsal surface dark yellow, darker at the margins; faint thin bands cross the forewing, wider and darker on the costa. Hindwing with faint, thin bands converging on the bi-lobed tornus with a short black tail. Ventral surface light yellow, maculation of the dorsal surface takes the form of thin, uniform reddish lines. Female: Unknown

Range (Fig.61). The species is known only from 2 specimens from Central and South Vietnam.

Material examined. Central Vietnam: 1♂ Ngoc Linh Nature Reserve, Kon Tum Prov. (ALM). **South Vietnam:** 1♂ Col du Da Tronm, Lam Dong Prov., 1225m (MNHN).

Dodona maculosa phuongi Monastyrskii & Devyatkin, 2000
Fig. 61

Dodona maculosa phuongi Monastyrskii & Devyatkin, 2000, p.488 (Pl. 21a figs. 3, 4).

This subspecies is known from a single specimen from Ba Be National Park in Bac Can Province, North Vietnam. The holotype male is in the MSU.

Diagnosis. The subspecies differs from nominate *D. maculosa* from China in "a faintly developed yellow streak in the cell of the forewing, more diffused spots on the dorsal surface, and the pure white markings on the ventral surface, which in the nominate species are mostly yellow" (Monastyrskii & Devyatkin 2000).

Discussion. *Dodona maculosa* Leech, 1890 was described from China (Ichang) as a species. In Tierreich (1928), Stichel made *maculosa* a subspecies of *D. eugenes*. Comparison of the types of *D. maculosa* and *D. eugenes* as well as the genitalia confirms the original status of this taxon, which thus becomes *Dodona maculosa* Leech, 1890, reinst. stat.

Habitat and biology. The Ba Be National Park is set among the limestone hills north of Hanoi. This phenotype appears to be rare. Date: June.

Range (Fig.61). The nominate subspecies is distributed throughout southwest China to Vietnam north of the Red River. Subspecies *phuongi* is known only from the type locality.

Dodona deodata Hewitson, 1876
Figs 17, 18, 61.

Dodona deodata Hewitson, 1876, Ent. Mo. Mag., 13:151.

Dodona deodata was described from a male from Moulmein, south Burma. The type is in the BMNH, London.

Diagnosis. Male (Fig.17). Dorsal ground color dark brown, both wings crossed by a white 6 mm wide median band, narrowing at the forewing costa to a point, and on the hindwing narrowing to a point towards the anal angle with a black lobe and pointed tail as an extension of vein Cu3. Some sympatric individuals are paler with extension of the white areas over much of the wing. Female (Fig.18). As male, but with more extensive white areas.

Discussion. Vietnam material examined is identical to specimens from Thailand and Laos.

Habitat and biology. Local, rare. Date: April.

Range (Fig. 61). The nominate subspecies is distributed from southern Burma through the Malay Peninsula and Thailand to Laos and Vietnam.

Material examined. North Vietnam: 1♂ Muong Nhe, Lai Chau Prov. (ALM). **South Vietnam:** 1♂ km 8 Route Darlac (Dalat?) (CJC); 1♀ Cat Tien, Lam Dong Prov., 700m (ALM); 2♂♂ 1♀ Bao Loc, Lam Dong Prov. (MNHN).

Dodona lecerfi Fruhstorfer, 1914, **n. stat.**
Figs. 13, 14, 15, 16.

Dodona deodata lecerfi Fruhstorfer, in Seitz, 1914, Vol. 9 , p.779, fig. 141b.

Dodona lecerfi was described from a male from Vinh, Annam (Central Vietnam). Although originally placed as a subspecies of *D. deodata*, examination of the morphology suggests it should be raised to species status. The type (Figs 13, 14) was located by me in the Vieux Collection, MNHN, and has been placed in the type collection of that institution.

Diagnosis. Male (Figs. 13, 14, 15). Forewing length 23mm. Dorsal wing ground color dark brown. Forewing median area crossed with a narrow, white irregular band, from cell to inner margin. Hindwing dorsad with a white median band 5mm wide at the costa narrowing to a point before the tail, and below M3 often infused with light orange scaling (Fig.15). Ventral ground color light brown with wide markings. Female. Forewing length 25mm, wings broad and rounded convex to base, distal margin straight. Maculation identical to male, though width of discal band may vary.

Discussion. *D. lecerfi* is related to *D. deodata* and *D. longicaudata*, sharing the white medial band and similar pattern on the ventral surface. However, it can be immediately separated by the extension of the narrow discal band to the anal angle, infused with orange scaling on the hindwing (Fig. 15), although this can be minimal, as in the type (Fig. 13). The male forewing distal margin is longer and female margin straighter. The dark bands on the ventral surface of both sexes are lighter and broader. Examination of the male genitalia of the three species shows many differences. *D. deodata* and *D. longicaudata* have a deeply bifurcated and pointed terminus on the transtilla, whereas in *D. lecerfi* (Fig. 54) it is wider and less bifurcated. *D. deodata* has a proportionately longer tegumen and small, rounded saccus and *D. longicaudata* narrower and longer valvae. In the female genitalia, the ductus bursae of *D. lecerfi* is long, narrow and straight, whereas in *D. longicaudata* and *D. deodora* it is wider, more robust with a ventral protrusion opposite the exit of the ductus seminalis.

Habitat and biology. This species is endemic to Central Vietnam. It is rare in collections. Nothing is known of its habits.

The white banded *Dodona* have always been a source of confusion and are in need of a general revision. In the literature (e.g. Pinratana, 1988) all the white *Dodona* are treated as seasonal forms. Examinationof the genitalia, however, suggests that they involve several distinct species. Three of these have been identified for Vietnam, *D. deodata*, *D. longicaudata* and *D. lecerfi*.

Material examined. Central Vietnam: 1♂ "Grande Bute, Annam" (MNHN); 2♂♂ Annam Caleu, N. Maumer 1921 (MNHN); 2♀♀ Annam 1924 (Fournier) (MNHN); 1♀ Lam Dong, Bao Loc, 779m, 19-05-1974 (MNHN); 1♀ "Annam" (BMNH).

Dodona longicaudata Niceville, 1881, **reinst. stat.**
Figs. 19, 20.

Dodona longicaudata, Niceville, 1881. P. Asiat. Soc. Bengal, p.121.

D. longicaudata was described from a male from Assam. The location of the type is currently unknown. Fruhstorfer in Seitz (1914) placed *longicaudata* as a subspecies of *D. dodona*. However, examination of the facies and genitalia suggest that it is a valid species.

Diagnosis. Both sexes have a narrower white band on both wings, reaching 3mm on the male forewing and more infusion of the white areas with darker scaling. Ventral surface markings red-brown. Male genitalia differs from *D. deodata* in the longer tegument, wider valvae, and a longer and squared saccus.

Discussion. Material from Vietnam is identical to specimens from Assam and Burma. It has much the same range as *D. deodata*. Although not mentioned from Thailand it probably occurs there.

Range. Burma through Thailand to Vietnam.

Material examined. Central Vietnam: 1♂ Pu Mat Nature Reserve, Ngho An Prov., 1000m (ALM).

Genus *Abisara* C. & R. Felder, 1860

=*oenabarus* Toxopeus, 1926, *nom. nud.*

Abisara is the largest old world genus of riodinid butterflies, occurring from Africa throughout the tropical Oriental Realm to Weber's Line. The Oriental species are divided into three groups; the *echerias* group with the margin of the hindwing forming a dentate extension below M3; the *neophron* group with M3 on the hindwing extended into a pointed tail, and the *fylla* group with little or no extension. The butterflies included in this genus all have one to three black ocelli on the apex of the hindwing. They have a bouncy flight and land on dorsal leaf surfaces with wings halfway open, making a few jerky movements on the leaves when landed. They do not stay long before flying to another leaf. I have never seen them on damp earth. The larvae have been recorded on *Maesa*.(Johnson & Johnson 1980).

Abisara echerias Group

The *echerias* group consists of a large number of variable phenotypes that have created much confusion over the years. A semblance of order came with its revision by Bennett (1950). Unfortunately the British Museum collection has little material from Indo-China, so Bennett's work largely ignored this region. This gap was partially filled for the South Vietnamese fauna by Inuoé & Kawazoé (1964).

Abisara echerias echerias (Stoll, 1790)
Fig 21, 22, 62.

=*odin* (Fabricius, 1793)
=*coriolanus* (Fabricius, 1793) (Papilio)
=*xenodice* (Hubner, 1816) (Lycaena)
=*f. lydda* (Hewitson, 1865) (Sospita)
=*tonkiniana* Fruhstorfer, 1904
Papilio echerias. C. Stoll in Suppl. Cramer, 1790, Pap. Exot., 383, p140.

The nominate race of *echerias* in Vietnam was originally described as *tonkiniana* by Fruhstorfer, of which the type is in the BMHN. The type of A. *echerias* is lost.

Diagnosis. Male (Fig.21). Small (wing length 17 mm), uniformly darker discal area on both wings bordered distad by a darker line and then by a light uniform band; two additional lighter parallel narrow submarginal and marginal bands follow; variable black spots bordered in white are present in cells M1–M2, M2–M3, and C1–C2 on the ventral surface. Female (Fig.22). Dorsal surface like the male, but lighter with larger spots and more rounded forewings. Postdiscal area of the forewing ventral surface with straight, uniform bands.

Discussion. The North Vietnamese population was originally described by Fruhstorfer (1904) as *A. tonkiniana* from a male from the Manson mountains. This population differs from the nominate subspecies that ranges from southern China to Hong Kong only in having generally larger spots. However, the range of variation is within that of the nominate subspecies. Nominate *echerias* borders with subspecies *paionea* to the west and south of Vietnam.

Habitat and biology. The nominate subspecies inhabits lowland forests to 1100m (Tam Dao), and usually is seen along forest paths. The life history has been recorded from Hong Kong. (Johnson & Johnson 1980). Dates: December, March. Uncommon.

Range (Fig 62).The nominate subspecies occurs from Hong Kong through southeast China to Vietnam north of the Red River to northern Laos and Thailand.

Material examined. North Vietnam: 1♂ 1♀"Tonkin" (BMNH); 1♂ 1♀ Song Chai, "Tonkin" (BMNH); 2♀♀ Haut Lon Ca – Vinh, Tonkin (BMNH); 1♂ 1♀ Tam Dao, 1100m (ALM); 1♂ 1f Bai Tu Long National Park, Islands (ALM); 10♂♂ 2♀♀ Bien Hoa region, Tonkin (MNHN).

Abisara echerias paionea Fruhstorfer, 1914
Figs. 23, 24, 62.

=*Abisara echerias notha* Bennett, 1950, **n. syn.**

Abisara kausambi paionea Fruhstorfer, 1914, in Seitz, Grossschetterlinge der Erde,v.9, p782.

Abisara echerias paionea was described by Fruhstorfer from the Karen Hills in Burma as a subspecies of *Abisara kausambi* C & R. Felder. The type is in the BMNH.

Diagnosis. Male (Fig.23). Differs from nominate *echerias* in larger size, more pointed forewing, dark reddish brown ground color and broader bands and larger spots; dorsal side of forewing with post median bands clearly seen. Dorsal surface uniform reddish brown. Ventral surface with post median bands parallel; second band meeting marginal band at the tornus. Female (Fig.24). Differs from nominate *echerias* in the less angled median band and lighter submarginal area above M3.

Discussion. Bennett (1950) transferred *paionea* from *A. kausambi* to *A. echerius* based on the similarity of the male genitalia. He also described subspecies *notha* from a female from Chiem Hoa, central North Vietnam that had been designated by Fruhstorfer (1904) as the female of *A. meta* Fruhstorfer, 1904. Bennett considered the male of *A. meta* to be a subspecies of *A. saturata* (see below). Bennett recorded an additional female of *notha* from Phuc Son in Central Vietnam. In South Vietnam, another female was located by Inuoé and Kawazoé at Bu Dang, 210km north of Ho Chi Minh City. No males were examined by either author, which is surprising as they can be quite common. My examination of males and additional females left no doubt that these refer to subspecies *A. e. paionea*, being identical to specimens from Thailand (Pinratana 1988, p.38). Pinratana suggests that *paionea* is the wet season form of *echerias*. It is true that their capture dates appear to correspond to the seasons and the genitalia are identical. However, the ranges do not overlap and *paionea* is the only form recorded in central to South Vietnam. There are specimens that appear intermediate with *A. echerias echerias* from Tam Dao and Bien Hoa north of Hanoi, and a rather aberrant female from Cuc Phuong National Park. Whether or not *paionea* in fact constitutes a separate species will have to await the study of more material and field observations.

Habitat and biology. Found from sea level to 1500m in primary and secondary forest and disturbed habitats. The female from Cuc Phuong was captured in open grass beside the road. Dates: March, April, June, July, September. Local but common.

Range (Fig. 62). Found throughout eastern Thailand, Laos, and Central to South Vietnam. In Thailand, it is recorded from Chaing Mai, Chanthaburi, Nakhon Ratchasima (Pinratana 1988) and in Laos, from Vientiane, Xiang Khouang, and Thakhek (Osada *et al.* 1999).

Material examined. North Vietnam: 1♀ (Type) Chiem Hoa, Tuyen Quang Prov. (BMNH); 12♂♂ 2♀♀ Hoa Binh, Tonkin (MNHN); 1♀ Tam Dao, Vinh Puc Prov. (ALM). **Central Vietnam:** 2♂♂ Ba Na, Quang Nam Prov. (ALM); 4♂♂1f Kon Ka Kinh, Gia Lai Prov. (ALM); 1♂ Phong Dien, Thua-Hien Hue Prov. (ALM); 1♂ 1♀ Pu Mat Nature Reserve, Ngne An Prov. (ALM); 1♂ Ngoc Linh Nature Reserve, Kon Tum Prov. (ALM). **South Vietnam:** 1♂ Bha Trang Nature Reserve, Khanh Hoa Prov. (ALM); 1♀ Bao Dam District, Lam Dong Prov. (ALM).

Abisara saturata meta Fruhstorfer, 1904
Figs. 25, 26, 62.

=*siamensis* Fruhstorfer, 1904
=*annamitica* Fruhstorfer, 1904

Abisara meta Fruhstorfer, 1904, Berl. Ent. Zeit, 48:285.

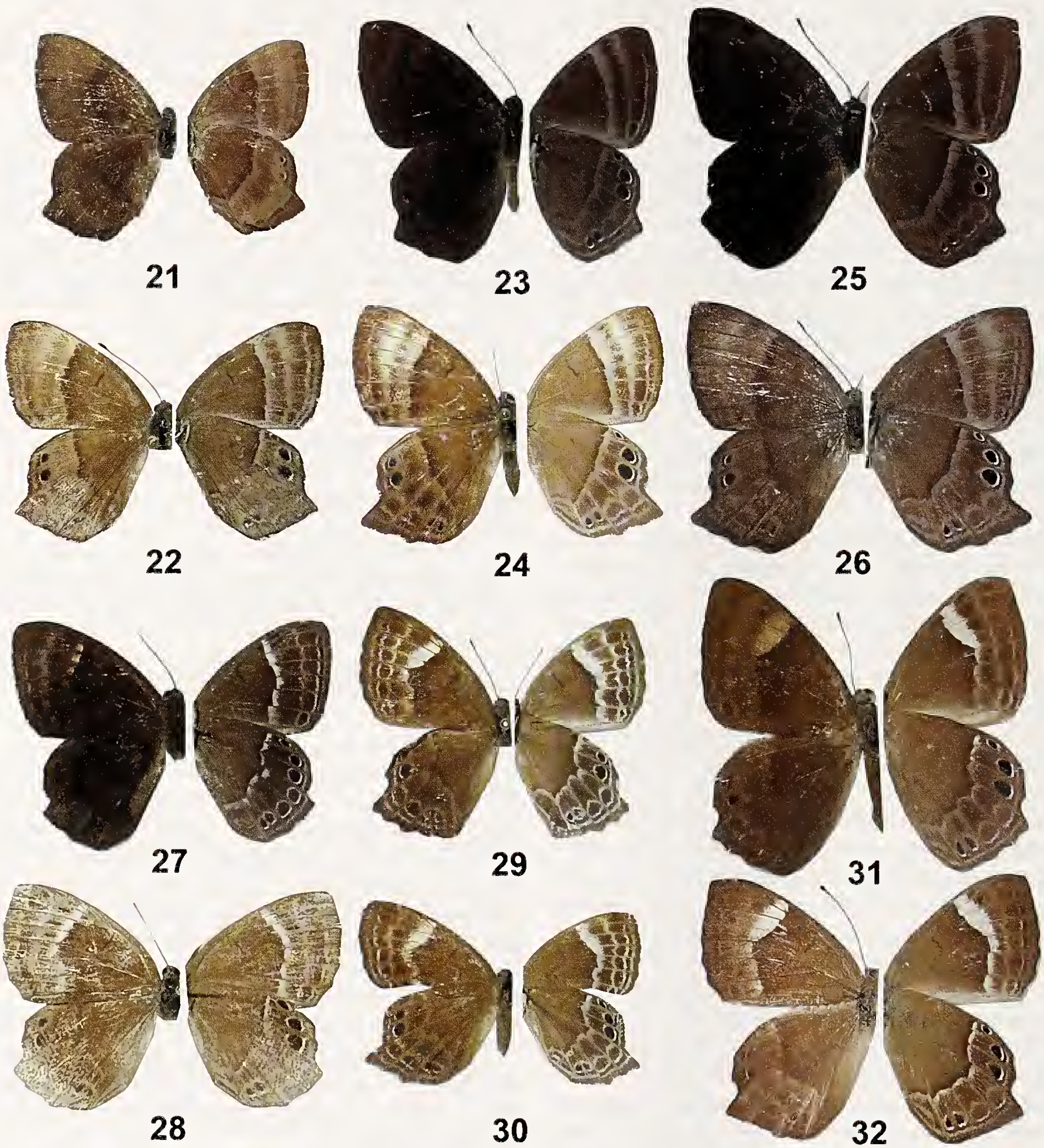
Fruhstorfer described *A. meta* from a male and female from Lang Son Province, Vietnam, just south of the Chinese border. The male of this taxon was made a subspeeies of *Abisara saturata* by Bennett (1950) based upon the male genitalia. Nominate *A. saturata* was described from Hainan island. The type of *A. meta* is in the BMNH.

Diagnosis. Male (Fig. 25). Differs from *A. e. paionea* in its slightly larger size, and on the ventral surface of the forewing, the discal and postdiscal bands are straighter, the postdiscal band is curved distad at the tornus toward the submarginal band, instead of being straight. On the hindwing, the discal band is rounder as it approaches the inner margin, whereas on *paionea* it jags more sharply. Female (Fig. 26). Differs from the male in the lighter brown ground color and the more pronounced tail on the hindwing. It differs in addition from *paionea* females in the darker ground color, and absence of lighter scaling along the veins in the postdiscal area of the hindwing. Females from Thailand have a light tan subapical area that is lacking in Vietnamese specimens.

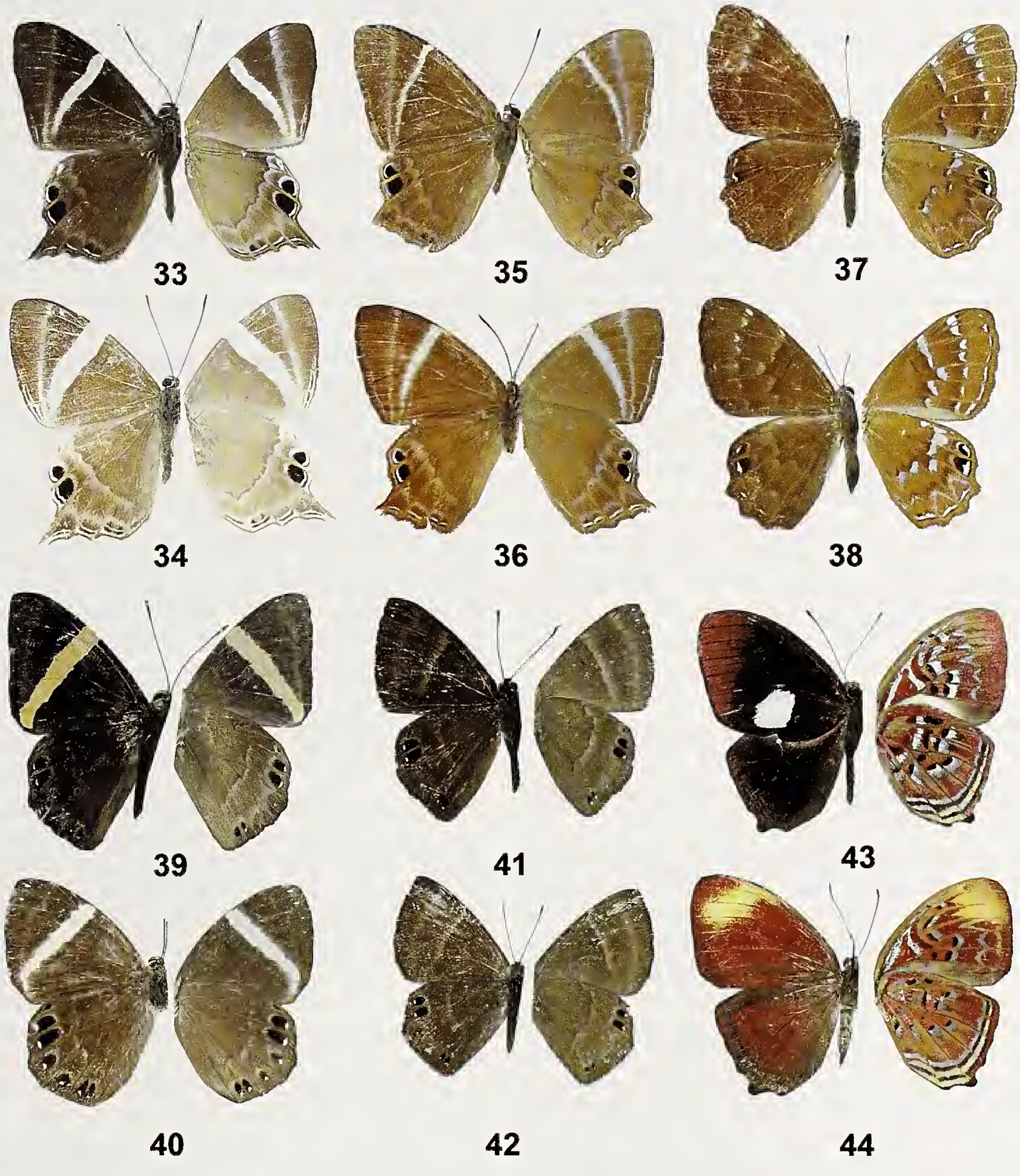
Habitat and biology: Unknown.

Range (Fig.62). North Vietnam along the Chinese border, to northern Thailand.

Material examined. 1♂ (holotype) Than-Moi, Lang Son Prov. (BMNH); 4♂ 4♀♀ Mont Du Haute Song Chai, Lao Cai Prov. (MNHN).



FIGS. 21–32. **21.** *Abisara echerias echerias* male, **22.** *Abisara echerias echerias* female, **23.** *Abisara echerias paionea* male, **24.** *Abisara echerias paionea* female, **25.** *Abisara saturata meta* male, **26.** *Abisara saturata meta* female, **27.** *Abisara abnormis* male, **28.** *Abisara abnormis* female, **29.** *Abisara bifasciata angustilineata* male, **30.** *Abisara bifasciata angustlineata* female, **31.** *Abisara latifasciata* male, **32.** *Abisara latifasciata* female.



FIGS. 33–44. **33.** *Abisara neophron chelina* male, **34.** *Abisara neophron chelina* female, **35.** *Abisara attenuata* male, **36.** *Abisara attenuata* female, **37.** *Abisara burnii timaeus* male, **38.** *Abisara burnii timaeus* female, **39.** *Abisara fylla magdala* male, **40.** *Abisara fylla magdala* female, **41.** *Abisara freda* male, **42.** *Abisara freda* female, **43.** *Paralaxita telesia boulleti* male, **44.** *Paralaxita telesia boulleti* female.

Abisara abnormis Moore, 1884
Figs. 27, 28, 62.

Abisara abnormis, Moore, Proc. Z. soc. London, 1884, p. 532, pl. XLIX, fig. 3.

This species was described from a male from Moulmein, Burma, currently in the BMNH.

Diagnosis. Male (Fig. 27). Forewing length 1.7cm. Dorsal surface of forewing uniform dark brown with a row of four white spots below the apex. Ventral surface has a thin, white discal band across both wings. South Vietnamese specimens differ from the type in the smaller white spots on the forewing and narrower white bands on the ventral surface. The genitalia are identical to Burmese specimens. Female (Fig. 28). Like the male but with lighter ground color and wider and more extensive white markings, particularly on the forewing.

Habitat and biology. Inhabits forest areas of the Mekong delta, 50m, and the Chau Doc Mountains on the Cambodian border.

Range (Fig. 62). The species is found across Indochina from Burma and southern Thailand to South Vietnam. Thailand localities are Nakon Ratchasima and Phetchaburi (Pinratana 1988).

Material examined. South Vietnam: 1♂ Saigon (MNHN); 1♂ 1♀ Montagnes Chau Doc, Cochinchine, An Giang Prov. (MNHN).

Abisara bifasciata angustilineata Inuoé & Kawazoé, 1965
Figs. 29, 30, 55, 62.

Abisara bifasciata angustilineata Inuoé & Kawazoé, 1965, p323, figs 4, 5, plate II figs 9, 10, 11, 12.

This taxon was described from a male and two females from Trang Bom, Dong Nai Province, South Vietnam.

Diagnosis. Male (Fig.29). Forewing length 1.7 cm. Dark discal area angled sharply at M3 on both wings; distad of this is a variable white band, on the forewing wider above M3 to the costa. Ventral surface with a variable white discal band crossing both wings and white scaling along the veins. Genitalia (Fig.55) with broad pointed process on the vinculum and the lateral lobes on the transtilla short and rounded, identical to *A. bifasciata* angulata from Burma. Differs from typical *A. abnormis* on the dorsal surface of the forewing in having a wider white band above M3, and on the ventral surface in having white scaling from the discal band outlining the veins crossing the sub-margin. Female (Fig.30). Like the male but with lighter ground color and wider white lines. Genitalia identical to *A. b. angulata*.

Habitat and biology. Inhabits primary forest areas in middle altitudes. Dates: Feb, April, May, July, August. Local, but can be common.

Range (Fig.62). The species is found from India to Indochina with 5 subspecies. The subspecies angustilineata occurs in Central and South Vietnam to Laos (Vientiane, Oudomsay, Osada *et al.* [1999], plate 104 under *Abisara abnormis*) and to southeast Thailand.

Material examined. 2♂♂ 1♀ Dar Lac Road, km 8, Dac Lak Prov. (CJC); 1♀ Puom Bekheng, Dac Lac Prov. (CJC); 2♂♂ darker males, Dar Lac Road, km 8 (CJC).

Abisara latifasciata Inuoé & Kawazoé, 1965, **n. stat.**
Figs. 31, 32, 56, 62.

Abisara geza latifasciata Inuoé & Kawazoé, 1965, p325, fig.6, plate II fig 15,16.

This taxon was described by Inuoé & Kawazoé (1965) from a male originating from Dalat (Thac Pongour). An additional paratype is from Dinh Quan, Ding Nai Province, South Vietnam.

Diagnosis. Male (Fig.31). *A. latifasciata* is close in appearance to angustilineata, but can be distinguished by its larger size (forewing length 2.3cm), darker ground color, reduced white markings on the distal area of both wings, both dorsal and ventral surfaces, and a yellowish subapical patch on the forewing dorsal surface. Genitalia (Fig. 56) with broad pointed process on the vinculum and the lateral lobes on the transtilla short and rounded with rounded lateral process; valvae deeply bifurcated with long tips. Female (Fig. 32). Wider white discal bands than the male and more rounded forewing tips.

Discussion. This taxon was described as a subspecies of *A. geza*, a designation the authors do not explain. It appears to be more closely related to *A. bifasciata* Moore, particularly since, as the authors point out, the male genitalia share the pointed process on the vinculum and the short and rounded lateral lobes of the annellus. The comparison of the genitalia of *latifasciata* (their Fig. 21) with that of nominate *geza* from Java suggest that *latifasciata* is distinct. Indeed, Inuoé & Kawazoé (1965) illustrated the male genitalia (their Fig. 6), but did not compare this with Bennett's (1950) illustration of that of *geza* (his Fig. 10). As *bifasciata angustilineata* and *latifasciata* were encountered at the same locality and date, I consider them distinct species, and raise *latifasciata* to species rank.

Habitat and biology. Inhabits primary evergreen forest in the middle elevations in South Vietnam. Dates: February, April, May.

Range (Fig.62). The species is found in South Vietnam and Laos (Xaignabouri) (Osada *et al.* 1999, under *A. bifasciata*).

Material examined. 5♂♂ 1♀ Dar Lac Road, km 8 (CJC); 4♂♂ 7♀♀; "Vietnam" (BMNH).

Abisara kausambi kausambi C. & R. Felder, 1860
Fig. 62.

Abisara kausambi [C. & R.] Felder, 1860. Wiener ent. Monatschrift 4(12): 397.

This taxon was described from Malaysia. The type is in the BMNH.

Diagnosis. Male. Dorsal surface crimson brown, paler at the apex of the forewing, ventral surface bands straight on both wings, not angled; on the holotype, the hindwing margin is only slightly indented at M3, not pointed. Female. Lighter, with submarginal band widening to form a broad, pale buff subapical patch. Margin of hindwing more pointed than male at M3.

Discussion. Inuoé & Kawazoé (1965) determined 2 females as belonging to this species. Both the genitalia and description of the facies are in line with Bennett's key. This is the first record for *A. kausambi* from Indo-China, and outside of Sundaland and the Malay peninsula, although Pinratana (1988) says it is found in peninsular Thailand, without illustrating specimens or giving a locality. Corbet & Pendlebury (1992) record it from Malaya. No Vietnamese specimens were seen by me, so this taxon is treated here as belonging to the nominate subspecies until more material can be examined.

Habitat and biology. According to Bennett (1950), the species inhabits primary forests. Inuoé and Kawazoé's captures were in July and August, at the height of the rains, a time when little collecting is normally done, which may explain its rarity in collections.

Range (Fig. 62). The species is found throughout the Greater Sunda Islands to Malaysia and is divided into 6 subspecies (Bennett 1950). The Vietnamese specimens are from Dinh Quan, Dong Nai Province, and Col de Blao, Lam Dong Province, both locations on Rte. 20, in South Vietnam.

Abisara neophron Group

Abisara neophron chelina Fruhstorfer,1904
Figs. 33, 34, 63.

=*neophronides* Fruhstorfer, 1914
=*f. gratius* Fruhstorfer, 1912

Abisara chela chelina Fruhstorfer, 1904, Berlin ent Z. 48(4): 283.

Indochinese material is generally attributed to subspecies *chelina* Fruhstorfer, 1904. Originally described as a subspecies of *Abisara chela* de Nicéville, (1886), it was transferred to *A. neophron* by Fruhstorfer, in Seitz, (1914). The type of *chelina* is in the BMNH.

Diagnosis. Male (Fig. 33). Easily recognized by a long, pointed white tipped tail on the hindwing formed by an extension of vein M3, and a 3mm wide white band crossing the discal area of the forewing from the costa and tapering just before the tornus. The hindwing has 2 prominent ocelli at the apex; the white discal band, reduced by the infusion of brown scaling, continues to the inner margin of the hindwing. Female (Fig. 34). Nearly identical to the male, only larger with slightly darker ground color and wider bands.

Discussion. Examination of a long series at the BMNH suggests that *chelina* differs from the nominate subspecies in its lighter ground color. The band width within populations varies considerably. Vietnamese specimens generally differ in having a narrower forewing medial band in the males and sharper markings on the ventral surface.

Habitat and biology. This species is locally common, and inhabits low to middle altitude evergreen forests, from 300 to 1500m. The males pereh in open areas beside trails. The life history and biology of the nominate subspecies in Nepal is described in Callaghan (1997). Dates: March, April, May, October.

Range (Fig. 63). This species is very widespread through the Oriental region, from Nepal through the Indian subcontinent, to Indochina and Peninsular Malaysia. Subspecies *chelina* is found throughout Indochina from Burma and Yunnan in China to Vietnam and Malaysia.

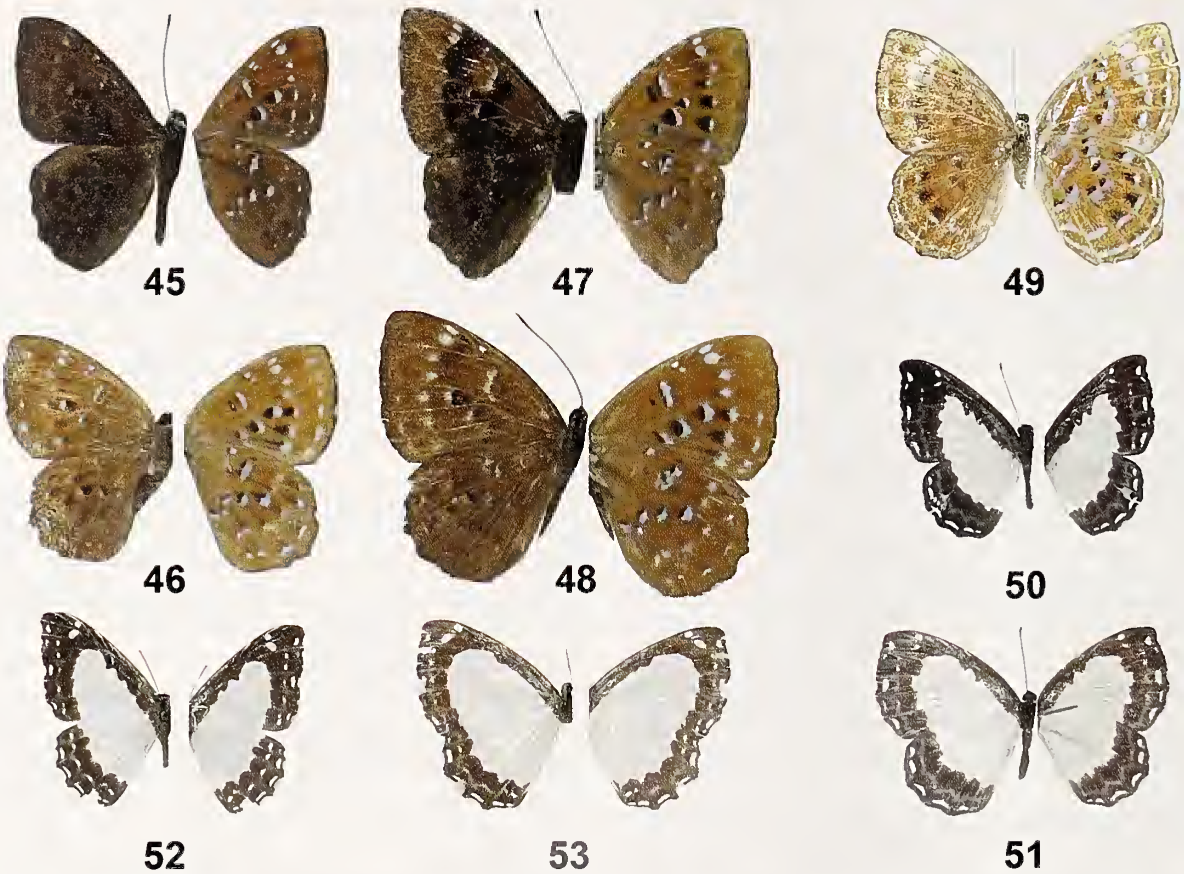
Material examined. North Vietnam: 1♂ Cuc Phuong, Ninh Binh Prov., 300m (CJC); 1♂ Muong Nhe Nature Reserve, Muong Nhe Prov., 460m (ALM), (AW); 2♂♂ 3♀♀ Pu Mat Nature Reserve, Nge An Prov., 1000m (FFI); 1♀ Huang Lien Nature Reserve, Lao Cai Prov., 1600m (AW); 1♂ 3♀♀ Tam Dao National Park, Phu Tho Prov., 1000m (TD). **Central Vietnam:** 2♂♂ 1♀ Vu Quang Nature Reserve, Ha Tinh Prov., 400–1500m (ALM); 11♂♂ 2♀♀ Ngoc Linh Nature Reserve, Kon Tum Prov., 1250–1850m (ALM). **South Vietnam:** 2♂♂ Hon Ba Provincial Nature Reserve, Khan Hoa Prov., 1200m (ALM); 1♂ Bao Dam District, Lam Dong Prov. (BHM); 2♂♂ Quang Nam Prov., 450m; 1♀ Kon Ka Kinh Nature Reserve, Gia Lai Prov. (AW).

Abisara attenuata (Tytler, 1915), **reinst. stat.**
Figs. 35, 36, 63.

Taxila attenuata Tytler, 1915, J. Bombay Nat. Hist. Soc. 23: 512, planche 2.

A. attenuata was described from a male from Assam. Stichel (1928) made this taxon a subspecies of *Abisara savitri* C. & R. Felder, 1860, undoubtedly due to its similar appearance. The examination of a long series of material and the types at the BMNH, as well as comparison of the genitalia, confirms their original designation as separate species.

Diagnosis. Male (Fig. 35). Easily recognized by the tails formed by an extension of vein M3 of the hindwing, and separated from *A. neophron* by the light, orange



FIGS. 45–53. **45.** *Taxila dora* male, **46.** *Taxila dora* female, **47.** *Taxila hainana* male, **48.** *Taxila hainana* female , **49.** *Laxita thuisto thuisto* female, **50.** *Stiboges nymphidia nymphidia* male, **51.** *Stiboges nymphidia nymphidia* female, **52.** *Stiboges elodinia* male, **53.** *Stiboges elodinia* female.

brown color of the dorsal surface, shorter tails and two narrow white discal bands on the forewing instead of one. It is easily distinguished from *A. savitri* by the forewing bands that diverge towards the costa instead of being parallel. Female (Fig. 36). Larger than the male and with rounded wingtips and slightly darker ground color.

Habitat and biology. Found in wet evergreen forests in middle altitudes. Uncommon.

Range (Fig. 63). The species is found from Assam to Laos near the Vietnam border, and Central to South Vietnam. Interestingly, Pinratana (1988) does not record it from Thailand.

Material examined. Central Vietnam: 1♂ 7♀♀ Kon Ka Kinh Nature Reserve, Gia Lai Prov. (AW). **South Vietnam:** 2♂♂ Dar Lac Road, km 8 (CJC); 1♀ Na Trang Provincial Nature Reserve, Khanh Hoa Prov. (ALM).

Abisara fylla group

Abisara fylla magdala (Fruhstorfer, 1904)

Figs. 39, 40, 63.

Sospita fylla magdala Fruhstorfer, 1904, Berlin ent Z. 48(4): 284.

Subspecies *magdala* was described from a male and female from Chiem Hoa in central North Vietnam. The types are in the BMNH.

Diagnosis. Male (Fig.39). Differs from the nominate subspecies in the narrower forewing discal band colored white to golden (In the nominate subspecies it is always yellow), larger ocelli on the hind-wing apex, and more prominent black spots on the margin of the hindwing. Female (Fig.40). Forewing band broader than the male, and always white. It differs from the nominate species in having larger hindwing marginal black spots.

Habitat and biology. Common in secondary forest and disturbed habitats along streams.

Range (Fig.63). The species ranges from Nepal to Yunnan, China and south to Vietnam and Laos. Subspecies *magdala* occurs in Vietnam, Thailand, and eastern Laos.

Material examined. North Vietnam: 2♂♂ 1♀ Pu Mat Nature

Reserve, Nghe An Prov., 1000m (ALM); 1♂ 1♀ Tam Dao National Park, Phu Tho Prov., 1000m (ALM); 1♀"Tonkin" (MNHN). **Central Vietnam:** 2♂♂ Ba Na, Quang Nam Prov., 1400m (ALM). **South Vietnam:** 1♂ 1♀ Nha Trang Provincial Nature Reserve, Khanh Hoa Prov., 600m (ALM).

Abisara burnii timaeus (Fruhstorfer, 1904)
Figs. 37, 38, 63.

Taxila burnii timaeus Fruhstorfer, 1904, Berlin ent. Z. 48(4): 278.

This subspecies was described from a male and female captured at Than Moi, Lang Son Province in northeast Vietnam. The type is in the BMNH.

Diagnosis. Male (Fig.37). Ground color dark red brown, as Fruhstorfer says, like "Munich beer". Dorsal markings, especially a submarginal row of spots are somewhat obliterated by brown scaling. Border of hindwing slightly scalloped between the veins. Ventral surface light brown-yellow with a prominent eyespot at the apex of hindwing. Female (Fig.38). Lighter ground color, white markings slightly more prominent than the male. Subspecies *timaeus* may be distinguished from the nominate subspecies by the reduced ocellus and fainter and more separated white markings.

Habitat and biology. Inhabits low altitude primary evergreen forest throughout Vietnam. Dates: April, July. It appears to be rare.

Range (Fig.63). *Abisara burnii* is found from the Naga hills in north Burma to central Laos, to west China (Sze-Tschuan) and Taiwan. Subspecies *timaeus* is confined to Vietnam and eastern Laos.

Material examined. North Vietnam: 2♀♀ Cuc Phuong National Park, Ninh Binh Prov., 400m (ALM). **Central Vietnam:** 1♂ Kon Cha Rang Nature Reserve, K'Bang District, Gia Lai Prov. (ALM). **South Vietnam:** 2♂♂ 1♀ Nha Trang Provincial Nature Reserve, Khanh Hoa Prov., 600–1400m (ALM).

Abisara freda Bennett, 1957
Figs. 41, 42, 63.

Abisara freda Bennett, 1957, The Entomologist 90(1125): Figs 1-4.

A. freda was described from a male specimen from Loimwe, southern Shan states in Burma. The type is in the BMNH.

Diagnosis. Male (Fig.41). Similar in appearance to *Abisara fylla*, but easily separated by the lack of the broad discal band on the forewing and its smaller size. Genitalia are similar to *A. fylla*. Female (Fig.42). Like male, but lighter ground color and rounded wing tips.

Habitat and biology. Disturbed mountain forest habitat along the Chinese border. Uncommon.

Range (Fig.63). Recorded from Burma through northern Thailand and Laos (Phong Saly, Osada *et al.* 1999) to North Vietnam.

Material examined. North Vietnam: 3♂♂ 2♀♀ Huang Lien Son, SaPa District, Lao Cai Prov., 1900m (ALM); 1♀ "Vietnam" (BMNH).

Genus *Taxila* Doubleday, 1847

Taxila dora Fruhstorfer, 1904
Figs. 45, 46, 57, 64.

Taxila dora Fruhstorfer, 1904, Berliner Entomol. Zeitschrift 48(4): 277.

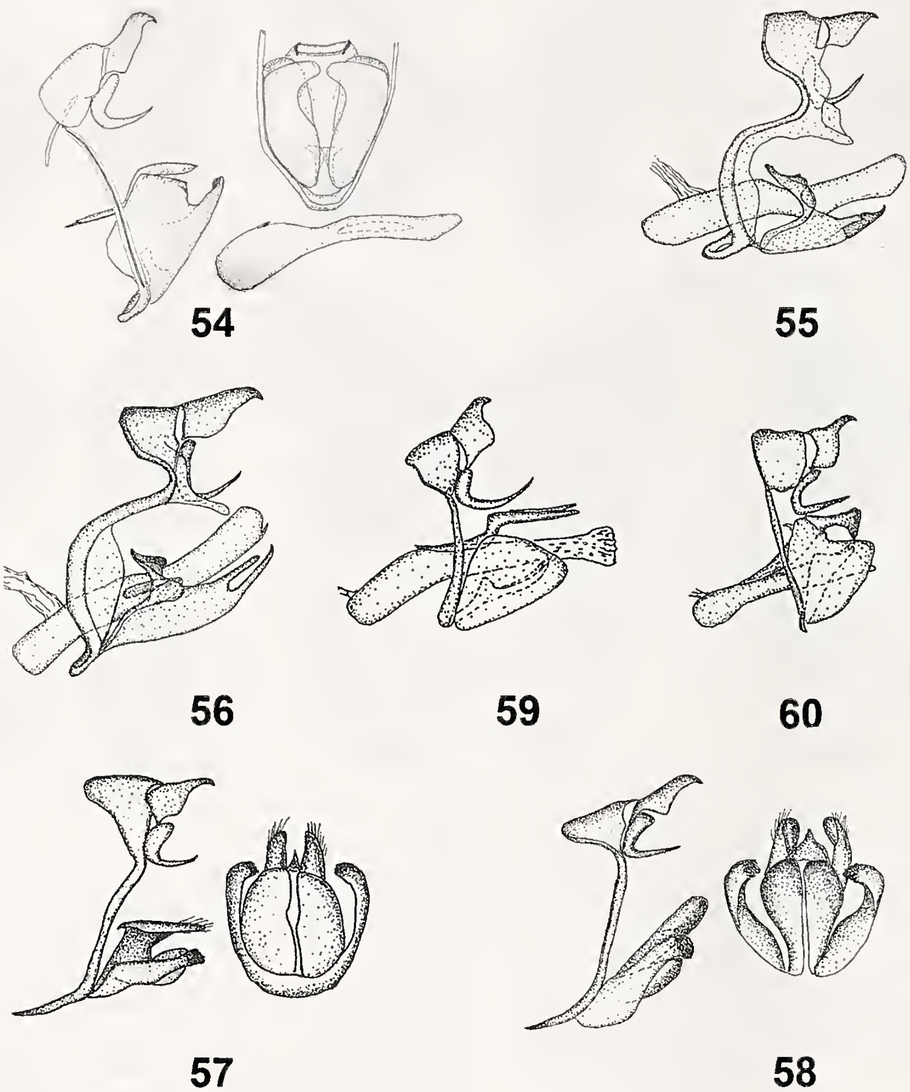
Fruhstorfer described *Taxila dora* from two males, one from Than-moi, Lang Son Province near the Chinese border, and the other from Chiem-Hoa, TuyenQuang Province, both locations in North Vietnam and north of the Red River. The holotype is in the BMNH.

Diagnosis. Male (Fig.45). Forewing length 19.5mm. Distal margins of both wings rounded; dorsal surface of forewing reddish brown, infused with variable black scaling below the cell; hindwing discal area reddish brown with costa and inner margin lighter. Ventral surface of both wings dull orange–red, two irregular parallel rows of small postmedian and submarginal white spots, and a blue streak edged distad with black at end of discal cell. Forewing cells M3-Cu1, Cu1-Cu2 with two blue spots edged basad in black; hindwing with lighter scales marking veins. Genitalia (Fig.57). Tegumen narrow, vinculum uniformly narrow; valvae flat with long external curved process with cornuti on tip; transtilla small, pointed with two lateral rounded, blunt processes. Female (Fig.46). Same pattern as male, but lighter brown, with a faint row of postmedial white spots. The ventral surface maculation appears clearly on dorsal surface. Genitalia with ductus bursae long, narrow; ostium bursae funnel shaped; signae on corpus bursae round with cluster of small cornuti.

Habitat and biology. *T. dora* can be encountered locally from sea level to 1700m in primary evergreen forest, and occasionally in secondary forest.

Range (Fig.64). This species is found from North through South Vietnam. Osada *et al.* (1999) record it from Boun Neua in Laos near the Chinese border.

Material examined. North Vietnam: 1♀ Haut Tonkin Bas Yunnan, (MNHN); 4♂♂ 1♀ Tonkin Hoa Binh (MNHN); 1♀ Tam Dao National Park, Phu Tho Prov. (ALM); 1♂ 1♀ Pu Mat Nature Reserve, Nghe An Prov. (ALM); 1♂ 4♀♀ Cuc Phuong National Park, Ninh Binh Prov., 400m (CJC); 2♂♂ Bai Tu Long National Park (ALM). **Central Vietnam:** 1♂ Vu Quang Nature Reserve, Ha Tinh Prov. (ALM); 1♂ Kon Cha Rang Nature Reserve, Gia Lai Prov. (ALM); 1♂ Quang Nam Prov. (ALM); 1♂ 1♀ Kon Ka Kinh Nature Reserve, Gia Lai Prov. (ALM); 1♀ Thua Thien Hue, Phong Diem District, Khe Lau Prov. (ALM). **South Vietnam:** 1♂ 4♀♀ Hon Ba Provincial Nature Reserve, Khanh Hoa Prov. (ALM); 2♂♂ Bao Dam District, Lam Dong Prov. (ALM).



FIGS. 54–60. Male genitalia: **54.** *Dodona lecerfi*, **55.** *Abisara bifasciata angustilineata*, **56.** *Abisara latifasciata*, **57.** *Taxila dora*, lateral and ventral views; **58.** *Taxila hainana*, lateral and ventral views; **59.** *Stiboges nymphidia nymphidia*, **60.** *Stiboges elodinia*.

Taxila hainana Riley & Godfrey, 1925, **n. stat.**
Figs. 47, 48, 58, 64.

Taxila dora hainana Riley & Godfrey, 1925, The Entomologist, 1925, p140, pl. III, fig. 4.

This taxon was described from a single male specimen from Five Finger Mountain, 700m, Hainan Island, China, as a subspecies of *P. dora*. The holotype is in the BMNH.

Diagnosis. Male (Fig. 47). Similar to *P. dora*, but larger, forewing length 22mm and more pointed. Dorsal surface light brown, forewing with a wide, diffuse black postdiscal band reaching from costa to dorsum and discal area to base infused with black scaling; hindwing with discal area to dorsum black; ventral surface lighter orange brown than *dora*, pattern similar. Genitalia (Fig. 58). General configuration similar to *dora*. Differs in the following respects: wider uncus and tegumen, end of tegumen wide and flat, lateral projections of transtilla wide and cup shaped, transtilla wide, external processes on valvae strongly curved inwards, but flatter internally. Female (Fig. 48). With similar pattern as male but paler, with a prominent postmedial row of white spots. Darker than the female of *P. dora*, larger (22mm vs. 19mm), and with more pointed forewings. Also, the first two

white spots of the postmedial row are larger. Genitalia. Ductus bursae a long, narrow tube; ostium bursae a small triangular plate.

Discussion. Comparison of the dorsal wing pattern and genitalia of specimens of *P. dora* with *P. hainana* suggests the two phenotypes are separate species. The two phenotypes are sympatric through most of their range in Vietnam with no indication of intergrades.

Habitat and biology. Inhabits primary evergreen forest from 220m to 1200m. Dates: March, April. Local.

Range (Fig.64). Hainan through south China to Vietnam and Laos. Osada *et al.* (1999) illustrate a male and female from Lak Sao in central Laos as "*Taxila dora*". One female from Yunnan, China (MNHN).

Material examined. North Vietnam: 4♂♂ 3♀♀ "Tonkin" (MNHN); 4♂♂ 1♀ Hoa Binh, Hoa Binh Prov. (ALM). **Central Vietnam:** 2♂♂ 1♀ Kon Cha Rang Nature Reserve, Gia Lai Prov. (ALM); 1♀ Vu Quang Nature Reserve, Ha Tinh Prov. (ALM). **South Vietnam:** 1♂ Nha Trang Provincial Nature Reserve, Khan Hoa Prov. (ALM); 1♂ Kon Ka Kinh Nature Reserve, Gia Lai Prov. (ALM).

Genus *Paralaxita* Eliot, 1978

Paralaxita telesia boulleti (Fruhstorfer, 1914)
Figs. 43, 44, 64.

Laxita boulleti Fruhstorfer, in Seitz, 1914, p.790, fig.141a, female.

Laxita boulleti was described from a single female from Siam (Mission Harmand). The holotype female was located by the author in the Ancienne Collection in the MNHN, Paris, and deposited in the type collection of that institution. The specimen has a label "Lakhon, Siam 1878, Dr Harmand". A type label with the currently recognized name was added. In addition, there is a male in the BMNH from north Siam with the label "Type". However, this specimen cannot be a type, having the date of capture as 1918, four years after the species was described.

Diagnosis. Male (Fig.43). Dorsal ground color black, forewings with dark reddish apex and distal area, and a large, round white spot below the discal cell on the inner margin. Ventral surface with two discal rows of unconnected blue-silver spots edged basad with black, forewing with a subapical yellow spot, hindwing with a black submarginal line edged basad in silver-blue and distad in black and yellow. Female (Fig.44). Dorsal surface carmine with a yellow subapical spot on the forewing. Differs from the nominate subspecies in the solid carmine color of the hindwing dorsal surface. Ventral surface as in male.

Habitat and biology. *P. telesia bouletti* inhabits primary evergreen forests from 400 to 1300m and flies throughout the year.

Range (Fig.64). The species ranges from northern Thailand through southern Indo-China and Sumatra, Borneo and Malaysia. Six subspecies have been described. Subspecies *bouletti* is found from Thailand across Laos (Lak Sao, Osada *et al.* 1999) to Central and South Vietnam.

Material examined. Central Vietnam: 2♂♂ Ba Na, Quang Nam Prov., 850m (ALM). **South Vietnam:** 1♂ Hon Ba Provincial Nature Reserve, Khanh Hoa Prov., 1300m (ALM); 2♂♂ 1♀ Nam Cat Tien National Park, Dong Nai Prov. (ALM); 2♂♂ 1♀ Nha Trang Provincial Nature Reserve, Khanh Hoa Prov. (ALM); Additional South Vietnam locality is Trang bom, Dong Nai Prov. (Inuoé & Kawazoé 1965).

Genus *Laxita* Butler, 1879

The genus *Laxita* was described by Butler with *Taxila teneta* Hewitson, [1861] as the type species. Only one species is found in Vietnam.

Laxita thuisto thuisto (Hewitson, 1860)
Figs. 49, 64.

Taxila thuisto Hewitson, 1860, Exot. Butt. V.4(2), pl37, figs. 5, 6.

Laxita thuisto was described from a male specimen from Singapore. A search for the type at the BMNH was unsuccessful. Four subspecies have been described.

Diagnosis. Male. Dorsal surface uniform dark brown. Ventral surface ground color reddish brown with a broken irregular post discal band of black spots edged distad in blue across both wings. A submarginal band of spots that are white on the forewing turn to black triangles edged distad with white/blue from Cu2 to the inner margin of the hindwing. On the margin is band of black lines bordered by white. Female (Fig. 49). Dorsal surface is reddish-brown; forewing with a subapical row of white spots to Cu2, the other markings reflecting those on the ventral surface. Ventral surface is identical to male.

Discussion. The row of white subapical spots on the females separates it from subspecies *sawaja* Fruhstorfer, 1914, which is characterized by a wide subapical bar. Vietnam material is nearly identical to Malaysian specimens.

Habitat and biology. Little is known of this butterfly due to its rarity in Vietnam. The single female specimen examined was captured in primary evergreen forest.

Range (Fig.64). The species is found from the Karen hills in Burma south throughout tropical Indo-China south to Sumatra and Borneo. Osada *et al.* (1999) illustrate a male and female from Thakhek and Xaignabouri in Laos.

Material examined. South Vietnam: 1♀ Tay Cat Tien National Park, Dong Nai Prov. (ALM); 1♂ "Cochinchine" (MNHN).

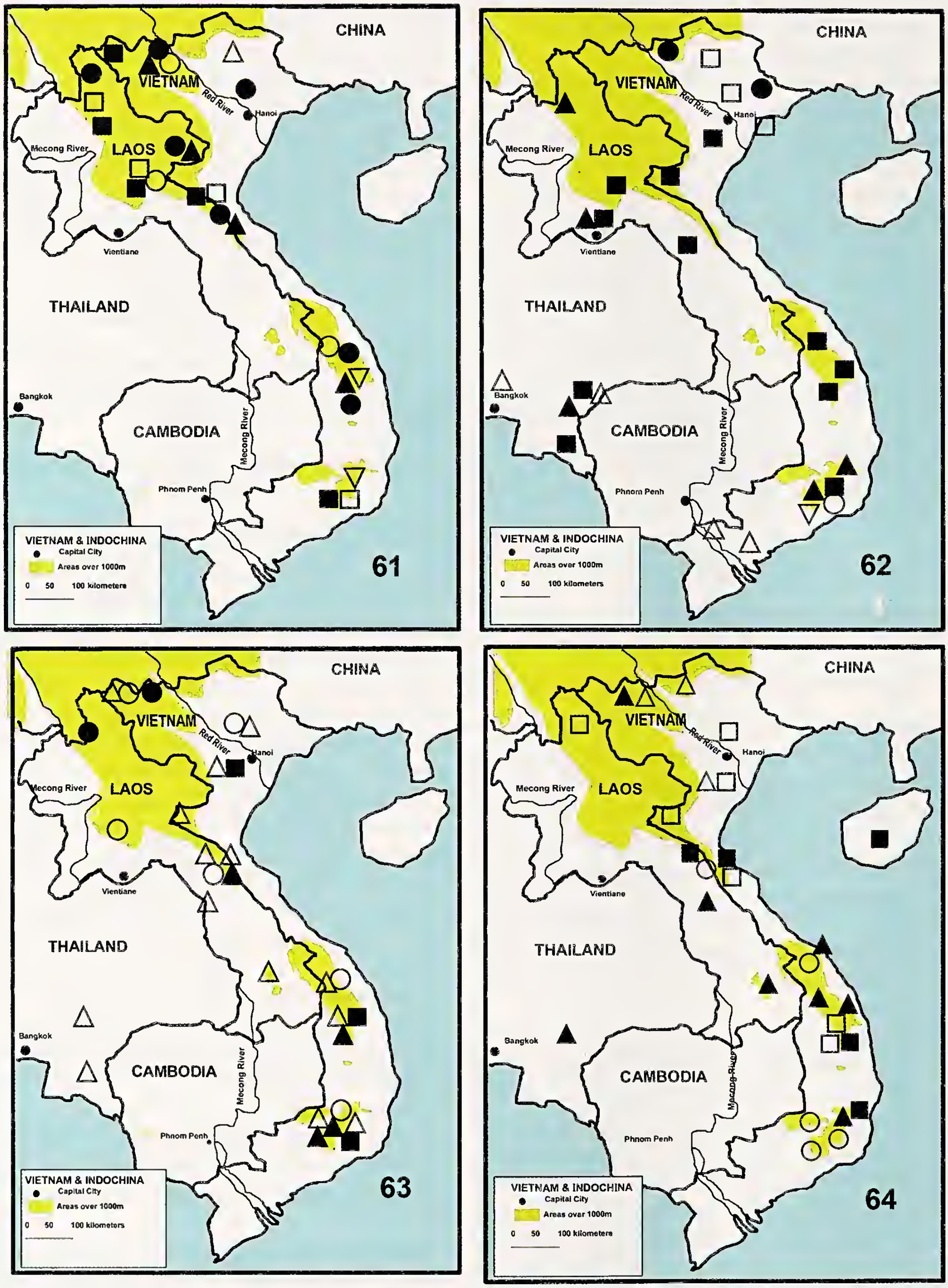


FIG. 61–64. **61.** Distibution map for *Dodona*: closed circles - *ouida palaya*, open circles - *adonira*, closed triangles- katerina, inverted open triangle - *speciosa*, open triangle - *maculosa* phuongi, open square - *egeon*, closed square - *deodata*. **62.** Distribution map for *Abisara echerias* group: *echerias* - open squares, *paionea* - closed squares, *saturata meta* - closed circles, *bifasciata angustilineata* - closed triangles, *abnormis* - open triangles, *latifasciata* - open circles, *kausambi kausambi* - inverted triangle. **63.** Distribution map for *Abisara neophron* and *fylla* groups: *neophron chelina* - open triangles, *attenuata* - closed triangles, *burnii timaeus* - closed square, *fylla magdala* - open circles, *freda* - closed circles. **64.** Distribution map for *Paralaxita*, *Taxila*, *Laxita* and *Stiboges*: *dora* - open squares, *hainana* - closed squares, *telesia boulleti* - open circles, *nymphidia* - open triangles, *elodinia* - closed triangles.

Genus *Stiboges* Butler, 1876

Stiboges nymphidia nymphidia Butler, 1876
Figs. 50, 51, 59, 64.

Stiboges nymphidia Butler, 1876.Proc. zool.soc. London :309, Plate XXII, fig. 1.

This species and genus were described from a female from Penang, Malaysia. The type is in the BMNH. Two subspecies have been described from Sumatra and Java.

Diagnosis. Male (Fig. 50). Transparent white with broad black borders on both wings surrounding a row of marginal white spots; white triangular area of forewing pointed towards the apex. Genitalia (Fig. 59). Small with beaked uncus, valvae large and broad with a pair of long pointed processes extending from the base caudad, transtilla with two narrower long pointed processes caudad; aedeagus broad and blunt; vesica with numerous small cornutae. Female (Fig. 51). Resembles male except for more rounded wingtips. Genitalia with ostium bursae very broad and rounded, ductus bursae long and tubular, palpi anales small, signae on corpus bursae round with small cornutae and slightly invaginated.

Habitat and biology. The species can be common in lowland primary forest from 300m. Their behavior as well as appearance is similar to neotropical riodinids of the genus *Nymphidium*. They have an irregular flight and rest on the ventral leaf surfaces with wings spread, which they flex slightly, a behavior unlike that of other Old World riodinids. In most Vietnamese localities, the butterfly is accompanied by a diurnal geometrid moth that closely resembles it and has the same flight and resting behavior.

Range (Fig. 64). *S. nymphidia* is found from Malaysia north through peninsular Thailand to Burma, Sikkim, Bhutan, Thailand, and Vietnam (Stichel 1930, BMNH). In North Vietnam, it inhabits the lowland forest from 300m just south of the Red River, to 2000m on the Chinese border. It has not been recorded from South Vietnam. Dates: March through September.

Material examined. North Vietnam: 10♂♂ 4♀♀ Cuc Phuong National Park, Ninh Binh Prov., 300m (CJC); 1♀ Mont Hte Song Chai, Tonkin (MNHN); 1♂ Huan Lien Song, Sa Pa District, Lao Cai Prov., 2000m (ALM).

Stiboges elodinia Fruhstorfer, 1914, **n. stat.**
Figs. 52, 53, 60, 64.

Stiboges nymphidia elodinia Fruhstorfer, 1914,. in Seitz, Grossschmetterling der Erde, v. p. 796, pl. 139c ("nymphidia")

Stiboges elodinia was described as a subspecies of *S. nymphidia* from a female from Sze-Tschuan, China. The holotype is in the BMNH.

Diagnosis. Male (Fig. 52). Similar to *S. nymphidia*, but with more pointed forewings. The distal borders slightly narrower, the apex of the white triangular area of the forewing rounded, and a row of tiny white submarginal spots present on both wings. Genitalia (Fig. 60) with uncus beaked, valvae flat, rounded ventrad, pointed dorsad, and with basad internal bifurcated process much smaller than in *S. nymphidia*; transtilla covered by a large, flat plate that is bifurcated caudad, with tips wide, down-turned and extending caudad over the aedeagus. Female (Fig. 53). Differs from the female of *S. nymphidia* in having wider white areas, smoother borders and small white submarginal spots. Genitalia. Ostium bursae with two small lateral flanges, ductus bursae long and narrow, flared slightly at the end. Signae round, slightly invaginated.

Discussion. *S. elodinia* can be separated from *S. nymphidia* by its narrower black border and generally larger size. Fruhstorfer noted that both wide- and narrow-bordered individuals are found in Tonkin, but ascribed the difference to wet and dry season forms. Examination of the genitalia of both phenotypes shows that they are in fact distinct species.

Habitat and biology. Inhabits primary forest above 1000m. Habits similar to *S. nymphidia*, but is considerably rarer. Dates March through September.

Range (Fig.64). The distribution of this species overlaps with that of *S. nymphidia*, with the result that most writers have considered it a subspecies or a seasonal form. It is found from west China to Vietnam in the mountains, west to northern Laos –Pak Munung (BMNH); Thakhek and Thateng (Osada *et al.* 1999), Thailand (Chang Mai, Nakkhon Nayok – Pinratana 1988), and probably south to Malaysia in the mountains (Corbet & Pendlebury 1978).

Material examined. North Vietnam: 2♀♀ Huang Lien Son Nature Reserve, Lao Cai Prov. (ALM). **Central Vietnam:** 1♂ Ba Na, Quang Nam Prov. (ALM). **South Vietnam:** 1♂ 2♀♀ Ngoc Linh Nature Reserve, Kon Tum Prov., 1600m (ALM); 1♀ Kon Cha Rang Nature Reserve, Gia Lai Prov. (ALM); Additional record: Col de Blau, Dong Nai Prov. (Inuoé & Kawazoé 1965).

Acknowledgements

I wish to thank the curators of the museums visited for access to the collections and type specimens under their care and the loan of specimens: Mr. Philip Ackery, (BMNH), Dr. Jacques Pierre (MNHN) and Dr. Wolfram Mey (ZMHU). Material and information was provided by my friend Alexander (Sasha) Montrievskii of the Vietnamese Russian Tropical Institute. An anonymous reviewer provided helpful comments on the manuscript. This work is dedicated to my friend and field companion Le Trong Dat who accompanied me on numerous excursions to Cuc Phuong National Park. My thanks also to the Cuc Phuong Park authorities who gave permission for work in the Park.

Literature Cited

Bates, H.W.J. 1867. Linn. Soc London, Zool. 9: 371–412.

Bennett, N.H., 1950. A revision of the *echerias* group of the genus Abisara. Entomologist, 83: 1–9, 34–42.

_____. 1957. A new species of *Abisara* from Burma. (Lepidoptera, Riodinidae). The Entomologist 90: 1, plate 2.
BUTLER, A.G. 1876. Descriptions of Lepidoptera from the collection of Lieut. Howland Roberts. Proc. Zool. Soc. Lond. 2: 308–310, 1 plate.
CALLAGHAN, C.J. 1997. The biology of *Abisara neophron neophron* (Hewitson 1860) from Nepal (Lepidoptera, Riodinidae). Bulletin de la Société Entomologique de France (Paris). 102(2): 129–132.
_____. 1997 (2000). A study of the riodinid butterflies of the genus *Dodona* in Nepal (Riodinidae). Journal of Research on the Lepidoptera 36: 1–15.
CORBET, A. & H.M. PENDLEBURY. 1992. The butterflies of the Malay Peninsula, 4th ed. Revised by J.N. Eliot. xiv + 578pp, 146+438 figs., Kuala Lumpur.
D'ABRERA, B. 1986. Butterflies of the oriental region. Part III Lycaenidae & Riodinidae. Hill House. 672 pp.
FELDER, C. & R. FELDER. 1860. Lepidoptera nova in paeninsula Malayica collecta. Wiener Ent. Monatschrift 4(12): 394–402.
FRUHSTORFER, H. 1904. Verzeichnis in Tonkin, Annam, und Siam gessamelten Nemeobiine und Libytheinae und Besprechnung verwandter Formen. Berl. Ent. Z. 48(4): 274–296.
_____, *In* Seitz, A. 1914. Grossschmetterlinge der Erde, 9: 772–798, pl. 138–141.
HEWITSON, W.C. 1857–1861. Illustrations of new species of exotic butterflies 2: [124] pp., 60 pls. London.
_____. 1874. Descriptions of new species of butterflies. Entomologist's Monthly Magazine 11: 56–58.
_____. 1876. Notes on Mr. Atkinson's collection of East Indian Lepidoptera, with descriptions of new species of Rhopalocera. Entomologist's Monthly Magazine 13(7): 149–152.
INOUE, S. & A. KAWAZOÉ. 1965. Riodinidae, Curetidae and Lycaenidae (Lepidoptera: Rhopalocera) from South Viet-Nam. Nature & Life in South—East Asia 4: 317–394.
JOHNSON & JOHNSON. 1980. This is Hong Kong: Butterflies. Government printer, Hong Kong.
LEECH, D. 1890. New species of Lepidoptera from China. The Entomologist 23: 26–45.
METAYE, R. 1957. Contribution a l'etude des Lepidopteres du Vietnam (Rhopalocera). Annals Faculte des Sciences. Saigon, 69–106, 3 pls.
MONASTYRSKII, A.L. & A.L. DEVYATKIN. 2000. New taxa and new records of butterflies from Vietnam (Lepidoptera, Rhopalocera). Atalanta 31(3/4): 471–492.
_____ & _____. 2003. New taxa and new records of butterflies from Vietnam, 2. Atalanta (June 2003) 34(1/2): 51–85, Pls V– IX.
_____ & _____. 2004. Butterflies of Vietnam: Satyridae.
MOORE, F. 1883. Descriptions of new Asiatic diurnal Lepidpotera. Proc. zool. Soc. London : 532, 2 plates 48 & 49.
NICEVILLE, L. DE & L. MARTIN. 1896. A list of the butterflies of Sumatra with special reference to the species occurring in the northeast of the island. J.Asiat. Soc. Bengal. 64 11: 357–555.
OSADA, S., Y. UÉMURA, J. UEHARA. 1999. *In* Y. Nishiyama (ed.). An illustrated checklist of the butterflies of Laos PDR. Mokuyo-sha, Tokio. 240pp.
PINRATANA, A. 1988. Butterflies in Thailand 4. Virarham Press, Bangkok. viii+216pp., 26 pls.
RILEY, N.D. & GODFREY. 1925. New Rhopalocera from Siam and Hainan. The Entomologist, 58: 140, planche 3.
SEVASTOPOULO, D.G. 1946. The early stages of Indian Lepidoptera. Part iv. J. Bombay Nat. Hist. Soc. 46: 253–269.
STICHEL, H. 1928. Lepidoptera: Nemeobiinae. Das Tierreich 51: 1–330.
_____. 1930. Lepidoptera Catalogus 30: Riodinidae I. W. Junk Berlin, 544pp.

Received for publication 18 October; revised and accepted 25 March 2008.

Journal of the Lepidopterists' Society
63(2), 2009,83-88

SEX BIAS ADULT FEEDING FOR GUMWEED (ASTERACEAE) FLOWER NECTAR AND EXTRAFLORAL RESIN BY A WETLAND POPULATION OF *LYCAENA XANTHOIDES* (BOISDUVAL) (LYCAENIDAE)

Paul M. Severns

Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis, OR 97331; severnsp@onid.orst.edu (author for correspondence)

and

Evrim Karacetin

Environmental Sciences Department, Oregon State University, Corvallis, OR 97331; present address: Erciyes University, Mühendislik Fakültesi, Çevre Mühendisli i Bölümü, 38039 Kayseri, Turkey

ABSTRACT. With the exception of some tropical genera, most butterflies rely on nectar as the primary adult resource and feed on non-floral resources, like tree sap, opportunistically. We found that an isolated wetland population of *Lycaena xanthoides* (Boisduval) (Lycaenidae) in western Oregon, USA, frequently uses both flower nectar and extra-floral resin of *Grindelia integrifolia* DC. × *G. nana* Nutt. var *nana* (Asteraceae) as an adult food resource. There were sex biases in nectar- versus resin-feeding preferences, with males feeding on *Grindelia* flower nectar more frequently than resin, and females feeding on resin more frequently than nectar. A combination of taste tests and sucrose estimates through a handheld refractometer suggested that the *Grindelia* resin may be a source of sugars, while a Kjeldahl analysis detected organic nitrogen at 2.6 ppm in the resin. We propose that the wetland population of *L. xanthoides* has either evolved or is evolving to use *Grindelia* resin as an adult resource because it is predictable in abundance over the landscape, unlike alternate non-floral adult resources.

Additional key words: nectar preference, *Grindelia*, butterfly behavior, adult butterfly resources, butterfly conservation

In temperate zones worldwide, butterflies typically rely on flower nectar as an adult energy source (Gilbert & Singer 1975; Boggs & Ross 1993; Boggs 1997a; Rusterholz & Erhardt 2000; Tooker *et al.* 2002) while feeding on non-floral resources such as feces, carrion, rotting fruit (Gilbert & Singer 1975), aphid honeydew (Rosenberg 1989; Corke 1999), and tree sap (Rosenberg 1989; Krenn *et al.* 2001; Warren 2005) appears to be largely opportunistic and likely supplemental to the primary diet. In tropical regions, specialization of adult butterflies on non-floral resources, like rotting fruit (DeVries *et al.* 1997; Krenn 2001; Knopp & Krenn 2003; Fischer *et al.* 2004; Molleman *et al.* 2005), is a strategy for acquiring resources infrequently used by temperate butterflies. Consumption of adult butterfly resources can directly influence population demographics by increasing fecundity (Boggs & Ross 1993; Boggs 1997a; Fischer & Fiedler 2001; Fischer *et al.* 2004), contributing to a longer lifespan (Hill & Pierce 1989; Karlsson & Wickman 1990; Fischer & Fiedler 2001), and providing energy for flight (Corbet 2000), which is related to both survival and fitness. Spatial and temporal aggregation of adult resources across a patchily distributed landscape of resources may also concentrate adult butterflies (Wiklund 1977; Peterson 1997; Schneider *et al.* 2003; Auckland *et al.* 2004), increasing opportunities for mating. For butterflies that have obligate associations with one or a few preferred adult resources, the combination of larval and adult resource distribution will determine whether a particular piece of habitat is suitable for colonization and population persistence. In the case of rare species that are of conservation concern, understanding what resources are preferred and the strength of the insect-resource interaction is essential for estimating habitat quality and providing appropriate targets for restoration (Severns *et al.* 2006).

In this paper, we report on the adult feeding behavior of a rare wetland population of *Lycaena xanthoides* (Boisduval) (Lycaenidae) in the Willamette Valley of western Oregon, USA, and its frequent use of an extra-floral herbaceous plant resin. We furthermore provide evidence that butterflies may derive sugars and nitrogen from this abundant, predictable extra-floral adult resource, and that the contribution of plant resin to the adult diet is an important interaction for local conservation planning in this butterfly species.

Materials and Methods

Study species. *Lycaena xanthoides* is a western North America butterfly primarily found in various dry habitats throughout northern Mexico, California, and southern Oregon (Scott 1986). However, two wetland populations of *L. xanthoides* occur in the Sacramento

Valley of central California (Shapiro 1974) and in the southern Willamette Valley of western Oregon (Severns & Villegas 2005). In these wetland populations, *L. xanthoides* females lay eggs that survive seasonal flooding and adults are restricted to the local wetlands (Severns *et al.* 2006; A.M. Shapiro pers. com. 2006). Western Oregon (Willamette Valley) *L. xanthoides* appeared to be historically rare and was presumed extinct until recently rediscovered (Severns & Villegas 2005). The butterfly population remains precariously small, with an estimated 97 total individuals (L90%=70, U90%=215) among three subpopulations (Ramsey & Severns 2008 in press). Immediately following its rediscovery in the Willamette Valley an attempt was made to understand butterfly-environment interactions that would enhance *L. xanthoides* restoration projects. A key interaction identified was that the Willamette Valley wetland population of *L. xanthoides* had a strong preference (> 85%) for flowers of perennial *Grindelia integrifolia* DC. × *G. nana* Nutt. var. *nana* (Asteraceae) plants (hereafter *Grindelia* and see Chambers 1998 for a taxonomic treatment) despite a conspicuous abundance of alternate nectar sources which other co-occurring butterfly species prefer (Severns *et al.* 2006). Although not reported previously (Severns *et al.* 2006), observations of female nectaring were not as common as male nectaring, despite a nearly equal number of males and females observed. Females commonly perched on the buds of *Grindelia*, but it was not noticed until the summer of 2006 that butterflies may use resin secreted by the plant as a food source. Resins secreted by *Grindelia* plants are generally most abundant on the flower heads of the plant, followed by the leaves, and then the stems (Hoffmann & McLaughlin 1986). A combination of dense glandular trichomes and resin canals (Hoffmann *et al.* 1984) produces conspicuous amounts of resin that appear on flower buds as either a white, sticky, viscous liquid, or a covering of clear, less viscous resin coating the phyllaries (Fig. 1). The clear, less viscous liquid appears while the glands are actively secreting resin, and as the resin dehydrates it becomes more viscous and sticky. *Grindelia* in western Oregon secretes resins beginning before the flower heads open and continues through the end of flower anthesis. *Grindelia* typically has 20 to 40 heads on a flowering plant but particularly large plants can have hundreds of flower heads. Each head has 20–50 disc flowers and 10–35 ray flowers that are open throughout the months of July, August, and September. Since the flight of *L. xanthoides* and *Grindelia* anthesis coincide, the abundance of flowering *Grindelia* plants is unlikely to be limiting in the study populations as flower heads easily number in the thousands.

Feeding observations and analysis. We were careful to record feeding on nectar or resin only if the proboscis was extended either into an open *Grindelia* disc flower or resin on the phyllaries of the inflorescence head. We recorded as many nectaring observations for each individual as possible. Because the study population of *L. xanthoides* is small, it was relatively easy to find identifying wing characteristics (e.g. wing tears, maculation differences, size, wing wear patterns, etc.) for individuals to be accurately followed. To avoid resampling of individuals, nectaring observations were gathered on two different occasions separated by 12 days. On both observation dates, male and female butterflies were encountered and at least 10% of the *Grindelia* heads contained open disc flowers.

We pooled the data within an individual to generate the per individual ratio of feeding on *Grindelia* resin or flower nectar (i.e. the number of flower nectaring observations for individual #1/ total number of feeding observations for individual #1). Ratios of nectar to resin feeding by individual were analyzed for adult resource feeding differences between sexes using a proportions test (Ramsey & Schafer 2002). We used a one-sided Wilcoxon signed-rank test to determine if within sex choice of food resource could be explained by random chance. We chose a non-parametric statistical test because data were not normally distributed and no other transformations (other than a rank transformation) improved the data distribution. Statistical analyses were performed using S-PLUS 6.1 for Windows Professional Edition (Insightful Corp 2002).

Simple sugar and nitrogen resin analysis. We gathered *Grindelia* flower buds from the field during the flight period of L. xanthoides, placed the buds in a

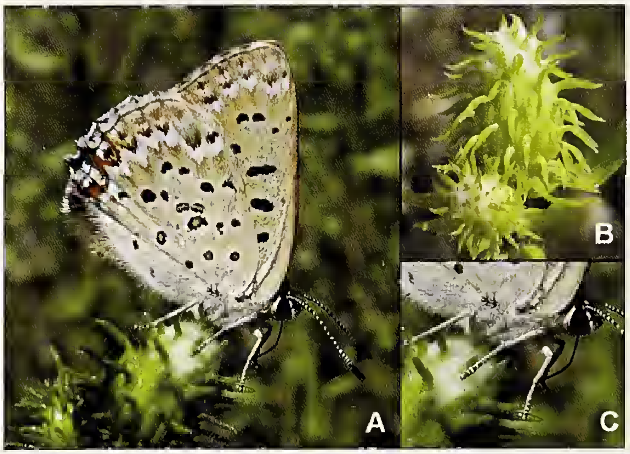


FIG. 1. **A**). Female *Lycaena xanthoides* feeding on *Grindelia* resin, **B**) a *Grindelia* bud covered with resin, and **C**) magnification of the proboscis placement from 1A.

plastic bag on ice, and transported the buds to a laboratory where the resin was extracted. We extracted resin by gently squeezing the phyllaries until a small droplet of resin, approximately 2-8 μL per head, was collected with a micropipette and placed into a centrifuge tube. Approximately 400 μL of exudate were collected from 50 unopened flower heads. The Brix concentration, an index of sucrose concentration, was estimated by taking the mean of five replicates (20 μL/sample) of pooled resin using an Atago ATC-1E handheld refractometer under manufacturer recommended conditions. Total inorganic and organic nitrogen (TKN) was estimated from 50 μL of pooled resin exudate by an acid Kjeldahl digestion (Strickland & Parsons 1972) which measures the amount of organic N in a given sample, excluding nitrites and nitrates (D'Elia *et al.* 1977).

RESULTS

Twenty individuals were reliably followed and the mean number of feeding observations per individual was 4.6 occasions (± 0.72 S.E.). A proportions test indicated that male *L. xanthoides* used flower nectar more frequently than females, while females fed on *Grindelia* resin more commonly than males (Fig. 2). Among the twelve males observed, most of the individuals preferred to forage on flower nectar and small number preferred resin (Fig. 2). Among the eight females observed, most preferred to feed on *Grindelia* resin instead of flower nectar (Fig. 2). No other butterfly species were observed feeding on *Grindelia* resin during the course of this study.

Chemical analyses of *Grindelia* resin suggest that there was a small amount of available resources for adult *L. xanthoides*. The Brix concentration was ca. 2.5% (± 0.3% SEM), suggesting that simple sugars, primarily sucrose, was an available resource in the resin (for a Brix scale comparison, a ripened banana has a Brix measurement between 10 and 12%). Total Kjeldahl nitrogen was 2.16 mg N/L of *Grindelia* resin, indicating that a small amount of organically bound nitrogen may be available for butterfly use.

DISCUSSION

Both sexes of Willamette Valley *L. xanthoides* fed on extra-floral *Grindelia* plant resin as well as flower nectar, and resin appears to have both simple sugars and a small amount of organically bound nitrogen available for use. The sugars are concentrated enough to be tasted by the human tongue (Severns pers. obs.) and the amount of organically bound nitrogen is positioned at the lowest end of ranges documented to support insect larvae (Mattson 1980). Although the observation number is

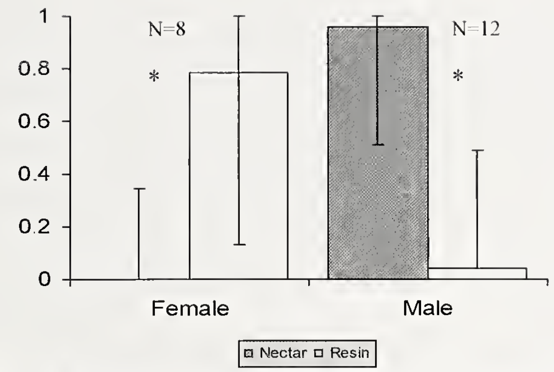


FIG. 2. Bar graph of median resin and flower nectar feeding with error bars representing the 1st and 3rd quartiles. A proportions test indicated that there was a difference in adult resource choice between male and female *L. xanthoides* ($Z = -5.093$, $p = 0.000000176$). The percentage of resin and flower nectar feeding instances indicates that females selected resin over nectar (Wilcoxon signed rank test: H0 = number of nectar visits < number of resin visits, $Z = 2.446$, $p = 0.0072$), while males preferred nectar over resin (Wilcoxon signed rank test: H0 = number of resin visits < number of nectar visits, $Z = -2.2713$, p-value: 0.0116). * = statistically significant difference between medians.

small, our data suggest that female Willamette Valley *L. xanthoides* preferred to feed on plant resin over *Grindelia* flower nectar, while males appeared to choose flower nectar over plant resin (Fig. 2). Rusterholz & Erhardt (2000) suggested that, within a species, male and female butterflies prefer different nectar species despite having the opportunity to feed from the same array of flowers. In some instances, sex-specific differences for nectar resources was linked to the availability of amino acids (Alm *et al.* 1990; Mevi-Schüutz & Erhardt 2002, 2003), which females may use to increase their fecundity (Murphy *et al.* 1983; Boggs 1997b). We do not know if any amino acids are available in *Grindelia* resin, but it does appear that soluble nitrogenous compounds are present in the resin, at low concentrations (*ca.* 2.16 mg/L of resin). *Grindelia* resin may also contain a low concentration of sugars as the solution tasted sweet and the Brix concentration of the resin was approximately 2.5%. Handheld refractometers, like the one used in this study, are known to measure compounds other than sucrose and do not measure other disaccharides and most simple sugars (Corbet 2003). Our Brix estimate of sugars in *Grindelia* resin may be an overestimate of some sugars but is also likely to underestimate others. A more rigorous chemical analysis is needed to understand the quantity and diversity of carbohydrate and nitrogen resources available for butterfly use in *Grindelia* resin and flower nectar.

Perhaps the most interesting aspect of *L. xanthoides* use of *Grindelia* resin as an adult resource is that the resins produced by *Grindelia* species are known to

contain chemical deterrents effective against lepidopteran larvae (Glendinning *et al.* 1998). It is unclear which compounds within the resin protect *Grindelia* plants from herbivory, but it may be due to grindelic acid (e.g. Mahmoud *et al.* 2000), a diterpene that is similar in structure to diterpenes found in trees of the Pinaceae (Langenheim 2003). This suggests the possibility that females may use secondary plant compounds to provision progeny with chemical predator deterrents. Since female *L. xanthoides* appeared to prefer resin over flower nectar while males displayed an opposite trend under the same environmental and site conditions (Fig. 2), gender associated resource selection may be due to chemical resources that are present or more plentiful in resin that are not in *Grindelia* nectar.

To our knowledge this is the only lycaenid population in temperate zones that has been documented to consistently use plant resin as an adult resource. Nymphalid butterflies in temperate zones do use tree resin opportunistically as an adult resource (Tolman & Lewington 1997; Scott 1986; Layberry *et al.* 1998; Corke 1999; Ômura & Honda 2003), but tree sap is not likely a dependable enough resource to annually support a butterfly population. For example, Rosenberg (1989) found that *Limenitis weidemeyerii* Edwards (Nymphalidae), *Vanessa atalanta* (L.) (Nymphalidae), and *Nymphalis antiopa* (L.) (Nymphalidae) fed on willow (Salix) tree sap from wounds created by yellow-bellied sapsuckers, *Sphyrapicus varius* (L.) (Picidae). For tree sap to be a dependable resource for butterflies, birds must be present annually, and tree wounding must be frequent and substantial enough for sap to be available throughout the butterflies' adult life span. In comparison to fruit production by tropical trees and resin production by *Grindelia* plants, the sap available from a wounded tree is a more unpredictable and limited resource. Willamette Valley *L. xanthoides* may be evolving a preference for *Grindelia* resin because it is a predictable, abundant resource in the remnant wetland prairies of western Oregon. Furthermore, this relationship between *Grindelia* resin and *L. xanthoides* may be more geographically widespread. *Lycaena xanthoides* in central California appear to prefer *Grindelia* flowers (Scott & Opler 1975; Shapiro & Manolis 2007) and may even be selective when given a choice of *Grindelia* species (Shapiro & Manolis 2007), but these authors did not note resin feeding. Other butterflies in the Willamette Valley either do not nectar on *Grindelia* flowers, or the species that do visit *Grindelia* flowers do not feed on resin (Severns pers. obs.). These observations suggest that *L. xanthoides* is the only local butterfly species using resin as a primary adult resource. However, it is possible that other temperate butterflies may use *Grindelia* resin as a food resource because members of this genus are common throughout western North America and arid areas of South America (Steyermark 1937), and at least one species is currently under cultivation for resin production in arid regions of North and South America (Timmermann & Hoffmann 1985; Zavala & Ravetta 2001). *Grindelia* species, with a broad geographic range, a predictable extra-floral resin resource, and relatively high local abundance may be a significant non-nectar adult resource for other Lepidoptera.

The Willamette Valley population of *L. xanthoides* is a target species for wetland conservation, in part due to its rarity and local wetland endemism (Severns & Villegas 2005; Severns *et al.* 2006). It was recently argued that there was an important association between the flower nectar of *Grindelia* and the distribution and habitat preference of adult butterflies (Severns *et al.* 2006). It appears that the importance of *Grindelia* may have been underestimated to the remaining Willamette Valley *L. xanthoides* population. In past studies (Severns & Villegas 2005; Severns *et al.* 2006), individuals that perched on *Grindelia* buds, that were likely feeding on resin, were not recorded doing so. Thus, the local dependence of *L. xanthoides* on *Grindelia* resources was likely underestimated. Since flower nectaring observations in past studies indicated that *L. xanthoides* nectared on *Grindelia* flowers ≈ 90% of the time without accounting for resin feeding, it is likely that interaction between Willamette Valley *L. xanthoides* and *Grindelia* as an adult resource is an obligate association. The natural extension of this information to management of the Willamette Valley *L. xanthoides* is that conservation and restoration of habitat must focus on two obligate butterfly resources – the host plant and *Grindelia* – for conservation projects to have the greatest chance of success.

Acknowledgements

We thank E. Bradford for helping gather field nectaring data, two anonymous reviewers for providing helpful comments on this manuscript, and S. Villegas (Eugene, Oregon District, Bureau of Land Management) for support of this project and access to the study site.

Literature Cited

Alm, J., T.E. Ohnmeiss, & J. Lanza. 1990. Preference of cabbage white butterflies and honeybees for nectar that contains amino acids. Oecologia 84:53–57.

Auckland, J.N., D.M. Debinski, & W.R. Clark. 2004. Survival, movement, and resource use of the butterfly *Parnassius clodius*. Ecol. Entomol. 29:139–149.

Boggs, C.L. 1997a. Reproductive allocation from reserves and income in butterfly species with differing adult diets. Ecology 78:181–191.

_____. 1997b. Dynamics of reproductive allocation from juvenile and adult feeding: radiotracer studies. Ecology 78:192–202.

_____. & C.L. Ross. 1993. The effect of adult food limitation on life history traits in *Speyeria mormonia* (Lepidoptera: Nymphalidae). Ecology 74:433–441.

CHAMBERS, K.L. 1998. Beware the hybrid gumplant. Oregon Flora Newsletter 4:9–10.

CORBET, S.A. 2000. Butterfly nectaring flowers: butterfly morphology and flower form. Entomol. Ex. Appl. 96:289–298.

_____. 2003. Net sugar content: estimating standing crop and secretion rate in the field. Apidologie 3:1–10.

CORKE, D. 1999. Are honeydew/ sap-feeding butterflies (Lepidoptera: Rhopalocera) affected by particulate air-pollution? J. Insect Conserv. 3:5–14.

D'ELIA, C.F., P.A. STEUDLER, & N. CORVAN. 1977. Determination of total nitrogen in aqueous samples using persulfate digestion. Limnol. and Oceanog. 22:760–764.

DEVRIES, P.J., D. MURRAY, & R. LANDE. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit feeding butterfly community in an Ecuadorian rainforest. Biol. J. Linn. Soc. 62:343–364.

FISCHER, K. & K. FIEDLER. 2001. Effects of adult feeding and temperature regime on fecundity and longevity in the butterfly *Lycaena hippothoe*. J. Lepid. Soc. 54:91–95.

_____, D.M. O'Brien, & C.L. Boggs. 2004. Allocation of larval and adult resources to reproduction in a fruit feeding butterfly. Funct. Ecol. 18:656–663.

GILBERT, L.E. & M.C. SINGER. 1975. Butterfly ecology. Ann. Rev. Ecol. Syst. 6:365–397.

GLENDINNING, J.I., S. VALCIC, & B.N. TIMMERMANN. 1998. Maxillary palps can mediate taste rejection of plant allelochemicals by caterpillars. J. Compar. Physiol. A 183:35–43.

HILL, C.J. & N.E. PIERCE. 1989. The effect of adult diet on the biology of butterflies. 1. The common imperial blue, *Jalmenus evagoras*. Oecologia 81:249–257.

HOFFMANN, J.J., B.E. KINGSOLVER, S.P. MCLAUGHLIN, & B.N. TIMMERMANN. 1984. Production of resins by arid adapted Astereae. Pp. 251–271, *In* B.N. Timmermann, C. Steelink, & F.A. Loewus (eds.), Phytochemical adaptations to stress. Plenum Press, New York.

_____ & S.P. MCLAUGHLIN. 1986. *Grindelia camporum*: a potential cash crop for the arid southwest. Econ. Bot. 40:162–169.

INSIGHTFUL CORPORATION. 2002. S-Plus 6.1 Windows Professional Edition. Seattle, Washington.

KARLSSON, B. & P.O. WICKMAN. 1990. Increase in reproductive effort as explained by body size and resource allocation in the speckled wood butterfly, *Pararge aegeria* (L.). Funct. Ecol. 4:609–617.

KNOPP, M.C.N. & H.W. KRENN. 2003. Efficiency of fruit juice feeding in *Morpho peleides* (Nymphalidae, Lepidoptera). J. Insect Behav. 16:67–77.

KRENN, H.W., K.P. ZULKA, & T. GATSCHEGG. 2001. Proboscis morphology and food preferences in nymphalid butterflies (Lepidoptera: Nymphalidae). J. Zoo. 254:17–26.

LANGENHEIM, J.H. 2003. Plant resins: chemistry, evolution, ecology, and ethnobotany. Timber Press, Portland, Oregon. 586pp.

LAYBERRY, R.A., P.W. HALL, & J.D. LAFONTAINE. 1998. The butterflies of Canada. University of Toronto Press, Canada. 280pp.

MAHMOUD, A.A., A.A. AHMED, T. TANAKA, & M. IINUMA. 2000. Diterpenoid acids from *Grindelia nana*. J. Nat. Prod. 63:378–380.

MATTSON, W.J., Jr. 1980. Herbivory in relation to nitrogen content. Ann. Rev. Ecol. Syst. 11:119–161.

MEVI-SCHÜTZ, J. & A. ERHARDT. 2002. Can *Inachis io* detect nectar amino acids at low concentrations? Physiol. Entomol. 27:256–260.

_____ & _____. 2003. Larval nutrition affects female nectar amino acid preference in the map butterfly (*Araschnia levana*). Ecology 84:2788–2794.

MOLLEMAN, F., H.W. KRENN, M.E. VAN ALPHEN, P.M. BRAKEFIELD, P.J. DEVRIES, & B.J. ZWANN. 2005. Food intake of fruit-feeding butterflies: evidence for adaptive variation in proboscis morphology. Biol. J. Linn. Soc. 86:333–343.

MURPHY, D.D., A.E. LAUNER, & P.R. EHRLICH. 1983. The role of adult feeding in the egg production and population dynamics of the checkerspot butterfly *Euphydryas editha*. Oecologia 56:257–263.

ÔMURA, H. & K. HONDA. 2003. Feeding responses of adult butterflies, *Nymphalis xanthomelas*, *Kaniska canace*, and *Vanessa indica*, to components in tree sap and rotting fruits: synergistic effects of ethanol and acetic acid on sugar responsiveness. J. Insect Physiol. 49:1031–1038.

PETERSON, M.A. 1997. Host plant phenology and butterfly dispersal: causes and consequences of uphill movement. Ecology 78:167–180.

RAMSEY, F.L. & D.W. SCHAFER. 2002. The statistical sleuth: a course in methods of data analysis. 2nd Ed. Duxbury Press, Belmont, California. 742pp.

_____. & P.M. SEVERNS. 2008 (in press). Persistence models for mark-recapture. Environ. Ecol. Stat. DOI 10.1007/s10651-008-0103-y

ROSENBERG, R.H. 1989. Behavior of the territorial species *Limenitis weidemeyerii* (Nymphalidae) within temporary feeding areas. J. Lepid. Soc. 43:102–107.

RUSTERHOLZ, H.P. & A. ERHARDT. 2000. Can nectar properties explain sex-specific flower preferences in the Adonis blue butterfly *Lysandra bellargus*? Ecol. Entomol. 25:81–90.

SCHNEIDER, C., J. DOVER, & G.L.A. FRY. 2003. Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. Ecol. Entomol. 28:219–227.

SCOTT, J.A. 1986. The butterflies of North America. Stanford University Press, Stanford, CA. 583pp.

_____. & P.A. OPLER. 1975. Population biology and adult behavior of *Lycaena xanthoides* (Lycaenidae). J. Lepid. Soc. 29:63–66.

SEVERNS, P.M. & S. VILLEGAS. 2005. Butterflies hanging on to existence in the Willamette Valley: a relict population of the great copper (*Lycaena xanthoides* Boisduval). Northwest Sci. 79:77–80.

_____, L. BOLDT, & S. VILLEGAS. 2006. Conserving a wetland butterfly: quantifying early lifestage survival through seasonal flooding, adult nectar, and habitat preference. J. Insect Conserv. 10:361–370.

SHAPIRO, A.M. 1974. The butterfly fauna of the Sacramento Valley, California. J. Res. Lepid. 13:73–82,115–122,137–148.

_____. & T.D. MANOLIS. 2007. Field guide to butterflies of the San Francisco Bay and Sacramento Valley regions. University of California Press, Berkley 345 pp.

STEYERMARK, J.A. 1937. Studies in *Grindelia*. III. Annals Missour. Bot. Garden 24:225–262.

STRICKLAND, J.D.H. & T.R. PARSONS. 1972. A practical handbook of seawater analysis. The Alger Press Ltd., Ottawa. 310 pp.

TIMMERMANN, B.N. & J.J. HOFFMANN. 1985. Resins from *Grindelia*: a model for renewable resources in arid environments. Pp. 357–368 *In* G.E. Wickens, J.R.

Goodin, and D.V. Field (eds.), Plants for Arids Lands. George Allen and Unwin, London.

TOLMAN, T. & R. LEWINGTON. 1997. Butterflies of Britain and Europe. Harper Collins Publishers, London. 528pp.

TOOKER, J.F., P.F. REAGEL, & L.M. HANKS. 2002. Nectar sources of day-flying Lepidoptera of central Illinois. Ann. Entomol. Soc. Amer. 95:84–96.

WARREN, A.D. 2005. Lepidoptera of North America 6. Butterflies of Oregon their taxonomy, distribution, and biology. Contributions of the C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins. 408 pp.

WIKLUND, C. 1977. Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* (Lepidoptera). Oikos 28:56–68.

ZAVALA, J.A. & D.A. RAVETTA. 2001. The effect of irrigation regime on biomass and resin production in *Grindelia chiloensis*. Field Crops Res. 69:227–236.

Received for publication 28 December 2007; revised and accepted 16 October 2008.

Journal of the Lepidopterists' Society
63(2), 2009,89–92

CATOCALA BENJAMINI UTE N. SSP. FROM SOUTHEASTERN UTAH (NOCTUIDAE: CATOCALINAE)

JOHN W. PEACOCK
185 Benzler Lust Road, Marion, OH 43302-8369, USA; email: lepnut@gmail.com

AND

DAVID L. WAGNER
Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3043, USA;
email: david.wagner@uconn.edu

ABSTRACT. *Catocala benjamini ute* **n. ssp.** is described from the high deserts of southeastern Utah. The three known locales in the vicinity of Moab, Utah represent a significant eastward range extension for the species. The new subspecies presumably feeds on *Quercus x pauciloba*, the principal oak growing at the locations where adults were collected.

Additional key words: *Catocala andromache*, *Catocala chelidonia*, *Quercus x pauciloba*.

Catocala benjamini was named by A. E. Brower in 1957 as a race of *Catocala andromache*. Its taxonomic status was essentially unchanged in Franclemont and Todd's (1983) checklist, wherein *benjamini* was recognized as a subspecies of *andromache* and grouped within the *Catocala delilah* complex of species—a group of about a half dozen, mostly western Nearctic, medium to small, yellow-winged, oak-feeding underwings. In 1982 Brower elevated *benjamini* to full species status, after noting that *Catocala andromache* and *C. benjamini* flew sympatrically over portions of their respective geographic ranges. In his treatment of the delilah group, Hawks (1986) also regarded *benjamini* to be a full species that ranged from desert mountain areas in California to southwestern Utah south through much of Arizona (presumably the insect occurs further south into Mexico). Here we extend the known geographic range of *benjamini* to eastern Utah (Fig. 9) and describe a phenotypically distinct geographic segregate that is associated with stands of *Quercus x pauciloba* [= *gambelii* × *turbinella*].

Catocala benjamini ute Peacock & Wagner **new subspecies**
Figures 1–3, 9

Diagnosis. Adults, especially females, average somewhat larger than the nominate subspecies and some Arizona populations (see Table 1). The orange-brown ground color of the forewing distinguishes most individuals—there are fewer charcoal, gray, steel-blue, and white scales or scale patches contributing to the forewing patterning (Figs. 1, 2, 4, 5). The subreniform spot tends to be pale orange and irrorated with dark scales; in the nominate subspecies the subreniform is consistently whiter (paler). The adterminal line in the forewing tends to be evenly undulate, and bounded distally by pale orange spots that frequently fuse (there are decidedly fewer black scales in the adterminal and terminal areas of the wing than in the nominate taxon); likewise on the underside of the forewing the adterminal area tends to be pale orange with reduced black scaling, and is rarely checkered as in the nominate subspecies (Figs. 5, 6). In about half the specimens we had for study, the forewing tends to be more triangular with a more acute apex (Fig. 1) than typical *Catocala benjamini benjamini* (Fig. 4). The venter of both wings tends to be a warmer (more saturated) pale orange than that of both nominate and Arizona populations (Figs. 3, 6). There are fewer dark scales suffusing the basal area of the hindwing common to other races of *benjamini*.

Description. *Forewing length*: male 22–23 mm, mean 22.4 mm, s.d. 0.5; female 24–27 mm, mean 25.3 mm, s.d. 1.1. Ground color: peach-orange-brown, with little charcoal, gray, and steel-blue scaling; white scales sparse on all wing surfaces. *Forewing*: nearly always with short basal line that ends over Cu; antemedial band double; running obliquely to inner margin, though often broken across lower half of wing; reniform spot small, diffusely margined with black; subreniform spot usually differentiated, peach-orange, lightly peppered with dark scales (white scales present in other populations absent); postmedian band complete, dodging outward distad to reniform spot, then running obliquely inward to costa; diffuse dark patch just distad of where pm line meets costa; subterminal line present as two blurry teeth near M1 and M2.; often small cluster of dark scales at forewing apex; scales mostly peach-orange distal to evenly scalloped adterminal line; venter with adterminal and apical areas decidedly peach-orange with reduced gray scaling (relative to the nominate subspecies). *Hindwing*: basal portion of wing with reduced dark scaling relative to the nominate subspecies; outer black band broad, at least twice the width of the inner black band; anal spot well developed, usually free of outer dark band; inner band often with well-developed anal hook that dodges toward inner margin above anal spot; fringe checkered where M and Cu reach margin. *Thorax*: dorsum warmer brown, not gray brown as in nominate subspecies. *Abdomen*: dorsum yellow-orange

FIGS. 1–6. *Catocala benjamini* adults. **(1)** *Catocala benjamini ute* holotype male, Arches Natl. Park, Grand Co., UT. **(2)** *Catocala benjamini ute* female, SR 313, Grand Co., UT. **(3)** *Catocala benjamini ute* male venter, Arches Natl. Park, Grand Co., UT. **(4)** *Catocala benjamini benjamini* male, Hualapai Mtn. Rd., Mohave Co., AZ. **(5)** *Catocala benjamini benjamini* female, near Payson, Gila Co., AZ. **(6)** *Catocala benjamini benjamini* male venter, near Payson, Gila Co., AZ.

with dark scales absent or sparse (compare Figs. 2 and 5).

Holotype male (Fig. 1): UTAH: Grand Co., Arches National Park, Balanced Rock Area, 1610 m, 7–8 June 2000, J. W. Peacock, 15W blacklight bucket trap, PMNH, Yale University, New Haven Connecticut.

Paratypes: 9 males and 17 females, 2 unsexed. UTAH: Grand Co., SR 313, 2.75 km W of jct. US 191, 7–8 June 2004, 1550 m, J. W. Peacock, bait trap,1 female (JWP); Arches National Park, Balanced Rock area, 1550 m, 7–9 June 2000, J. W. Peacock, 15W blacklight bucket trap, 1 male, bait trap, 1 male, 1 female (JWP); Arches National Park, Rock Pinnacles area, 1550 m, 7–8 June 2000, J. W. Peacock, bait trap, 1 male, 1 female (JWP); Arches National Park, Courthouse Rock area, [1280 m], 7–9 June 2000, J. W. Peacock, 15W blacklight bucket trap, 1 male, 3 females, bait trap, 1 male, 6 females (JWP); Arches National Park, vicinity of Courthouse Rock, 1435 m, 7–8 June 2004, at bait, 1 male, 1 female (JWP); Arches National Park, Courthouse Wash area, [1250 m],7–8 June 2000, J. W. Peacock, bait trap, 1 male, 2 females (JWP); Arches National Park, Petrified Dunes area, 1550 m, 7–9 June 2000, J. W. Peacock, bait trap, 2 males, 2 females (JWP). UTAH: San Juan Co., Canyonlands National Park, Squaw Flats Campground, 1710 m, 4 June 1994, B.C. Kondratioff and P.A. Opler, at light, 2 adults. All JWP on indefinite loan from Arches National Park.

Etymology. The subspecies is named after the Native Americans who most recently lived in this portion of Utah.

Life History Notes. *Catocala benjamini ute* is a denizen of high deserts and canyonlands of southeastern Utah (Figs. 7, 8). Our collection sites are from transitional areas between high desert sage communities and the lower reach of the juniper belt.

FIGS. 7–8. Habitat of *Catocala benjamini ute*. **(7)** JWP hanging bait trap at type locality: the low-lying green shrubbery at JWP's feet is the presumed host oak, *Quercus x pauciloba*. **(8)** Typical canyonlands habitat in Arches National Park, Moab, Utah.

Trees (junipers and oaks) are widely scattered, if present (Figs. 7, 8). The most widespread, and in some cases only oak at the colleetion sites is *Quercus x pauciloba* (= *Quercus undulata*) (Fig. 9), a tree of hybrid origin derived from *Q. gambelli* and *Q. turbinella* (USDA, NRCS. 2009; Michael Kuhns personal communication), a narrowly distributed large-acorned, scrubby oak of southeastern Utah and Arizona. We have not taken *benjamini ute* from stands of gambel oak in Arches and other nearby sites. Our collecting dates are all from the first ten days in June, and over these dates adults at light and in bait traps were in good to very good condition, indicating that adults had not been on the wing for long. Elsewhere the species is known to fly from late May through July with stragglers taken into September (Hawks 1986). Adults were relatively common in bait traps in 2000—eight to twelve adults were found in each of several bait traps after a single night of collecting. Numbers approached those of *benjamini* taken in bait traps in the Hualapai Mountains near Kingman, Arizona and in the Santa Rosa Mountains in Riverside Co., California in the same year. Fewer moths of both sexes were taken in the light traps run at the same locations. Numbers were lower when JWP returned in 2004—few moths were taken in either bait traps or at light despite comparable sampling intensity.

DISCUSSION

Catocala benjamini shows substantial differentiation across its geographic range in the American Southwest.

FIG. 9. Known distribution of *Catocala benjamini ute* (stars), *Quercus turbinella* (solid circles), and *Quercus x pauciloba* [*Q. gambelli* × *turbinella*] (open circles). Map reproduced from on-line version of Albee *et al.* (1988): http://earth.gis.usu.edu/plants/index.html (accessed January 2009).

Table 1. Forewing measurements for three populations of *Catocala benjamini* (in mm).

Taxon	Males				Females			
	no.	range	mean	s. d.	no.	range	mean	s. d.
benjamini benjamini (Mohave and Gila Counties, AZ)	14	20–23	22.3	0.8	13	21–25	23.8	1.2
benjamini "benjamini" (Riverside Co., CA)	6	20–22	21.0	0.9	6	21–24	22.8	1.0
benjamini ute (Grand Co., UT)	10	22–23	22.4	0.5	16	24–27	25.3	1.1

Hawks (1986) proposed manuscript names for three new subspecies from California and southern Arizona and here we describe a distinct phenotypic segregate from the most northeasterly portion of the moth's geographic range. The forewings of *Catocala benjamini ute* are more evenly yellow-orange and by comparison have fewer black, gray, and white scales, and the larger wingspan also distinguishes some females of this subspecies (Table 1). The three known localities for *C. b. ute* represent an eastward range extension for *benjamini* which was previously known only from Washington County, Utah, in the southwestern corner of the state.

It is not known if and to what extent the populations of *benjamini ute* in eastern Utah are disjunct from those of the nominate subspecies. JWP visited three other locations with *Quercus x pauciloba* in search of *benjamini ute* without success. These included seemingly suitable habitat in Canyon de Chelly, Apache County, Arizona; near Monument Valley Navajo Tribal Park, San Juan County, Utah; and a desert scrub area approx. 8 km W of Bluff, San Juan County, Utah. *Catocala chelidonia*, which JWP has collected in association with *benjamini* near Kingman, Arizona and *benjamini* in the Santa Rosa Mountains, California was common in bait traps at all three of these other locations (Canyon de Chelly, Monument Valley, and Bluff). While our failure to find *Catocala benjamini ute* at these three sites is (weakly) suggestive that *benjamini* from Grand County, Utah represents an outlying population, it is also true that many areas in southern Utah and northern Arizona have not been adequately surveyed. Elsewhere *Catocala benjamini* is associated with shrub live oak (*Quercus turbinella*) (Hawks 1986), one of the presumed parental lineages from which *Quercus x pauciloba* is derived (USDA, NRCS. 2009; Michael Kuhns personal communication). Johnson (1985) reared both *Catocala andromache* and *C. benjamini* ex ova on *Q. turbinella*, and wild populations of *C. benjamini* in California are often taken near stands of oak. As noted above, we have not yet found *C. benjamini ute* in gambel oak stands, and distributional data indicate that this host is not utilized (by members of the *Catocala delilah* complex).

ACKNOWLEDGEMENTS

We thank Paul Opler who first alerted us to the presence of *Catocala benjamini* in eastern Utah and shared his observations on the habitat and probable host. We are indebted to the Southeast Utah Group, National Park Service, for issuing a Scientific Research and Collecting Permit to JWP to conduct research on *C. benjamini* in Arches and Canyonlands National Parks (CANY-2000-SCI-0012, CANY-2002-SCI-0004, and CANY-2004-SCI-0014). Special thanks are due to Charles Schelz, biologist with the Southeast Utah Group, for his generous support of the study and for providing logistical, host plant, and other useful information. David Hawks and Larry Gall provided helpful comments on drafts of the manuscript. We are especially indebted to David who sent us his thesis on the biosystematics of the *delilah* group of *Catocala*. Andrea Farr and Alexia Lalande prepared the figures.

LITERATURE CITED

ALBEE, B.J., L.M. SHULTZ, & S. GOODRICH. 1988. Atlas of the vascular plants of Utah. On-line version: http://earth.gis.usu.edu/plants/index.html (accessed January 2009).

BROWER, A.E. 1957. Description of a new species and a new race of *Catocala* (Lepidoptera: Noctuidae). Bull. Brooklyn Entomol. Soc. 32: 184–186.

______. 1982. Change in status of *Catocala andromache* race "*benjamini*" (Lepidoptera: Noctuidae). J. Lepid. Soc. 36: 159.

FRANCLEMONT, J.C. & E.L. TODD. 1983. Noctuidae. Pp. 120–159. *In* R.W. Hodges *et al.* (eds.), Check list of the Lepidoptera of America north of Mexico, E.W. Classey Ltd. & The Wedge Entomological Research Foundation, Cambridge Univ. Press, Cambridge, United Kingdom.

HAWKS, D.C. 1986. The systematics and ecology of the *Catocala delilah* complex (Lepidoptera: Noctuidae). Unpublished Master's Thesis, Univ. California, Riverside. 119 pp.

JOHNSON, J.W. 1984 [1985]. The immature stages of six California *Catocala* (Lepidoptera: Noctuidae). J. Res. Lepid. 23: 303–327.

USDA, NRCS. 2009. The PLANTS database (http://plants.usda.gov, 13 January 2009). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Submitted 9 January 2008; revised and accepted for publication on 18 November 2008.

Journal of the Lepidopterists' Society
63(2), 2009, 93–99

LIFE HISTORY TRAITS, LARVAL HABITS AND LARVAL MORPHOLOGY OF A LEAFMINER, *COPTOTRICHE JAPONIELLA* (TISCHERIIDAE), ON AN EVERGREEN TREE, *EURYA JAPONICA* (THEACEAE), IN JAPAN

MASAKO OISHI

Department of Biological Sciences, Faculty of Science, Nara Women's University, Nara, 630-8506, Japan

AND

HIROAKI SATO

Department of Biological Sciences, Faculty of Science, Nara Women's University, Nara, 630-8506, Japan; email: scarab@cc.nara-wu.ac.jp

ABSTRACT. *Coptotriche japoniella* (Tischeriidae) is a leafminer that is specialized on the evergreen trees, *Eurya japonica* and *E. emarginata* (Theaceae). We investigated its larval habits, seasonal development and larval morphology on *E. japonica* in a red-pine forest on Takamado Hill, Nara, Japan. *C. japoniella* has a univoltine life cycle with six larval instars and a long larval period of 9 months from August to May of the following year. The larvae possess crochets on the ventral prolegs, as do other *Coptotriche* larvae associated with Rosaceae and Fagaceae. We discuss the relationship between voltinism of tischeriid species and leaf type (i.e. deciduous or evergreen) of their host plants, and also examine crochets on the ventral prolegs as a diagnostic character among the three tischeriid genera, *Coptotriche*, *Tischeria* and *Astrotischeria*.

Additional key words: adult longevity, larval crochets, leaf selection for oviposition

The family Tischeriidae is a small group of leafmining moths, consisting of 114 described species (Puplesis & Diškus 2003). As of the early 1990s, the family was considered to be made up of only one genus (i.e., *Tischeria* Zeller, 1839). Leraut (1993) erected a new genus, *Emmetia*, and indicated that larvae of the new genus possess ventral prolegs with crochets on the 3rd to 6th abdominal segments, whereas those of *Tischeria* (*s. str.*) have ventral prolegs lacking crochets. However, he did not examine any *Tischeria* larvae that are associated with Asteraceae or Malvaceae in North America. Unfortunately, he did not notice that his newly erected genus agreed with the genus *Coptotriche* that was erected by Walsingham (1890) for a North American species; *Coptotriche* had been commonly treated as a junior synonym of *Tischeria* (Braun 1972). Puplesis & Diškus (2003) made a cladistic analysis of the family on the basis of 34 characters, thereby recognizing three main lineages of generic rank: *Tischeria* (27 described species for the world fauna), *Coptotriche* (57 species) and *Astrotischeria* Puplesis & Diškus (30 species). They treated the genus *Emmetia* as a junior synonym of *Coptotriche* and erected the new genus *Astrotischeria*, which is distributed in North and South America. In their cladogram, *Tischeria* and *Astrotischeria* form a sister group. They also presented all known host plants of tischeriids. According to them, main host-plant families are as follows: Fagaceae, Rhamnaceae and Tiliaceae in *Tischeria*, Rosaceae and Fagaceae in *Coptotriche*, and Asteraceae and Malvaceae in *Astrotischeria*. Oddly enough, they made no reference to crochets of ventral prolegs by which Leraut (1993) characterized *Coptotriche* [=*Emmetia* in his sense] larvae. Consequently, crochets on the ventral prolegs remain unclear as a diagnostic character among the genera.

Compared with the taxonomic study of Tischeriidae, ecological study of the family has made little progress. Although voltinism of 18 species is known (Braun 1972; Opler 1974; Emmet 1976; Hisai 1979; Sato 1990; Puplesis & Diškus 2003), their life histories have not been examined in detail except for *T. ceanothi* Walsingham infesting *Ceanothus griseus* L. (Rhamnaceae) (Fasoranti 1984) and *T. ekebladella* (Bjerkander) infesting *Quercus robur* L. (Fagaceae) (Jordan 1995). Furthermore, parasitoid assemblages have been investigated in only three species, *T. ekebladella* (Jordan 1995), *T. quercifolia* Kuroko and *T. decidua* Wocke (Sato 1990).

Coptotriche japoniella Puplesis & Diškus is associated with the evergreen trees, *Eurya emarginata* (Thunb.) and *E. japonica* Thunb. (Theaceae). Before it was described as a new species by Puplesis & Diškus (2003), its life history had been investigated initially on *E. japonica* in Tokyo, Japan, by Hisai (1979). He reported that *C. japoniella* has a univoltine life cycle; the adults emerge in late May to June; the larvae hatch in late August, grow into 5th instar in late February of the following year, and pupate in mid-April to early June. Thus, *C. japoniella* has a unique life history in two

respects: (1) it is the only species to feed on plants of Theaceae among Tischeriidae, and (2) its larvae spend a long period of 9 months within the mine. In the current study, we investigated larval habits, seasonal development and leaf selection for oviposition according to leaf age in Nara, Japan. In addition, we examined larval morphology to consider whether crochets of prolegs can be used as a diagnostic character for *Coptotriche*. We have already published a paper on the parasitoid assemblage associated with *C. japoniella* (Oishi & Sato 2008).

MATERIALS AND METHODS

Study site. We carried out this study in a red pine (*Pinus densiflora* Siebold & Zuccarini, Pinaceae) forest on Takamado Hill (400 m a.s.l., 34°40'N, 135°52'E) near the urban area of Nara. The understory vegetation of the forest was dominated by *E. japonica*.

Host plant. *Eurya japonica* is an evergreen tree, occurring widely in China, Taiwan, Korea and from the middle to the southern part of Japan (Kitamura & Murata 1979). New leaves break buds in late April in Nara, Japan (Oishi & Sato, unpublished), and mature leaves can remain on the tree for 3 yr or more (Nitta & Ohsawa 1997; Oishi & Sato, unpublished).

Seasonal development of *C. japoniella* larvae. We randomly sampled about 30 leaves with an intact mine of *C. japoniella* from about 10 *E. japonica* trees at intervals of 10 d from 22 August 2003 to 17 June 2004. When we found a pupal exuvium protruding from the mine or a small slit at the edge, we classified the mine as an adult emergence. In other cases, we dissected mines with forceps to check whether they contained a larva or pupa. To determine the larval instar, we measured head widths of the larvae to the nearest 1×10^{-4} mm on the basis of digital photographs taken with a microscope at 50X. We scanned 10 leaves with an image scanner (CanonScan D1250U2F, Canon Co., Japan), and measured leaf and mine areas to the nearest 1×10^{-2} mm^2 with free software for image analysis (LIA for Windows32, ver. 0.376β1; Yamamoto 1997).

Leaf selection by females for oviposition according to leaf age. We selected 73 trees within a quadrat of 2 m x 15 m on 5 March 2003, and tagged three to six shoots of each tree (in total, 225 shoots). For these shoots, we checked leaves on the old nodes and leaves on the current-year nodes on 17 October, and recorded the number of newly emerged mines on each leaf. We recorded the number of mines for the same shoots again on 16 November of the following year.

Larval habits and adult longevity. We sampled 199 mined leaves from nine randomly selected trees on 22 November 2004, and put them individually in a plastic case in which a sheet of moistened filter paper was laid. We kept them in an incubator at a temperature of 15°C with 10L:14D photoperiod until 26 January 2005, 17°C with 10L:14D until 10 February 2005, and thereafter 20°C with 12L:12D. We observed larval behavior during rearing. To examine adult longevity, we transferred adult moths (8 males and 6 females) that emerged from 12 to 13 May 2005, separately, into a plastic case in which two absorbent cotton pieces with distilled water and 10% honey, respectively, were laid. Afterward, we counted dead adults every 24 hr until all the individuals died.

RESULTS AND DISCUSSION

Leaf selection for oviposition according to leaf age. The eggs of *C. japoniella* are cemented to the lower surface of the leaf. They are elliptic, 0.9 mm in length, 0.5 mm in width, with an iridescent semitransparent surface (Fig. 1A). Very few or no eggs were found on current-year leaves, but almost all eggs were laid on leaves aged 1 yr old or more (Fig. 2). Current-year leaves expanded during May, while adult females oviposited after June (see below). Thus, females exclusively select old leaves for oviposition.

Larval habits. The larva chews through the bottom of the egg, and directly enters the leaf tissue (Fig. 1A). It consumes the palisade tissue layer and the upper half of the spongy tissue layer (Fig. 1E), forming an irregular blotch mine with a yellowish green surface (Fig. 1B). It ejects frass through several arch-shaped slits on the lower surface of the mine. It feeds on the entire exuvium and leaves only the head capsule within the mine. When two mines on a leaf connect and the larvae encounter each other within the mine, cannibalism often occurs (Fig. 1D). The mature larva firmly backs the mine with silk, so that the upper surface of the mine is lined with a few folds (Fig. 1C). It also makes a crescent-shaped slit at the edge of the upper surface, and afterward closes it with silk. It pupates near the center of the mine. The pupa moves to the edge, and protrudes the upper part of its body from the slit at adult emergence.

Seasonal development. We estimated six larval instars from six peaks in the frequency distribution of larval head width (Fig. 3). Although the boundary between 1st and 2nd instars appeared to be obscure, it was confirmed by the existence of two head capsules remaining within the mine. However, Hisai (1979) mentioned that *C. japoniella* has five larval instars. He most likely missed the 3rd instar larvae because they made no field sampling in mid- to late September. Although Fasoranti (1984) and Jordan (1995) considered *T. ceanothi* and *T. ekebladella* to have four

larval instars, they did not seem to distinguish head capsules of 1st and 2nd instars, judging from the fact that the head-capsule width that they defined as the 1st instar's has a much larger coefficient of variance than those of other instars. Thus, *T. ceanothi* and *T. ekebladella* probably have five larval instars.

The 1st instar larvae hatched in mid- to late August, feeding on leaf tissue within the mine through the summer and early winter (Fig. 4B). They overwintered as 5th instars. Cessation of mine enlargement from December to March (Fig. 4A) indicates that 5th instar larvae scarcely consumed leaf tissue during the winter. Overwintered larvae resumed growing in early April, and pupated in mid-May to early June. The mean area of fully extended mines was 272.2 ± 31.8 mm^2 (mean ± SDs, n=10). Consequently, the larvae spent over 9 months within the mine.

Adult longevity and oviposition period. The adults emerged in mid-June (Fig. 2B). The mean longevity of adults under rearing conditions was 12.1 ± 2.03 days (mean ± SDs) for males and 14.7±1.21 days for females. Females already had mature ovaries 1 d after their emergence. These results suggest that oviposition of *C. japoniella* continues for 2 wk at most after adult emergence. Thus, it takes 2 months for the eggs to hatch in August, suggesting that eggs are in the state of aestivation after they are laid.

Life history traits. As mentioned above, *C. japoniella* is a univoltine leafminer with a long larval period of 9 months. As far as we know, *C. discreta* (Braun), which is distributed in North America and associated with evergreen oaks (*Quercus* spp.), is the

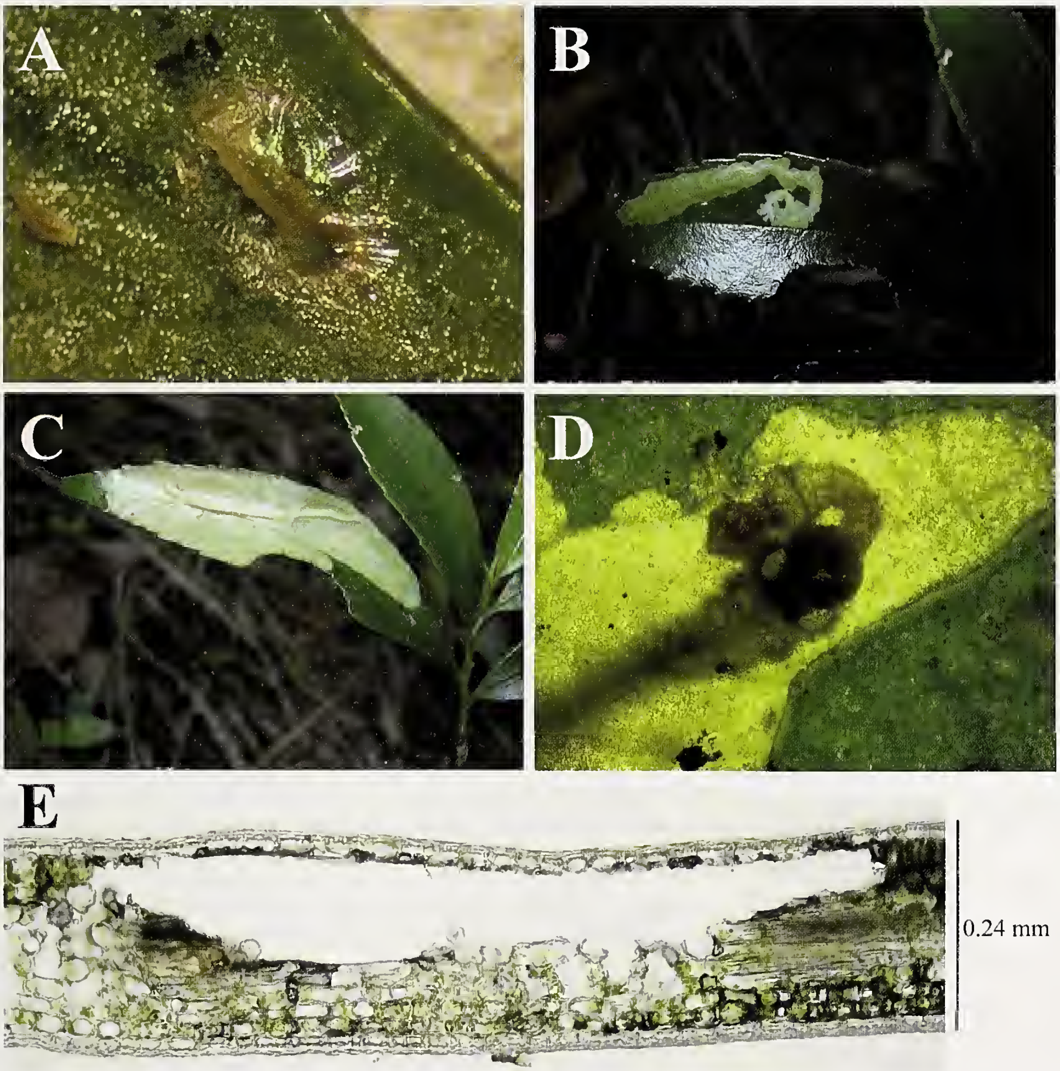


FIG. 1. Immature stages of *Coptotriche japoniella*. **A,** egg shell and newly hatched larva directly mining into mesophyll under the egg; **B,** irregular blotch mine of 5th instar larva; **C,** fully expanded mine lined with a few folds; **D,** larval cannibalism within a mine which was formed by two mines connected; **E,** transverse section of mine of 3rd instar larva.

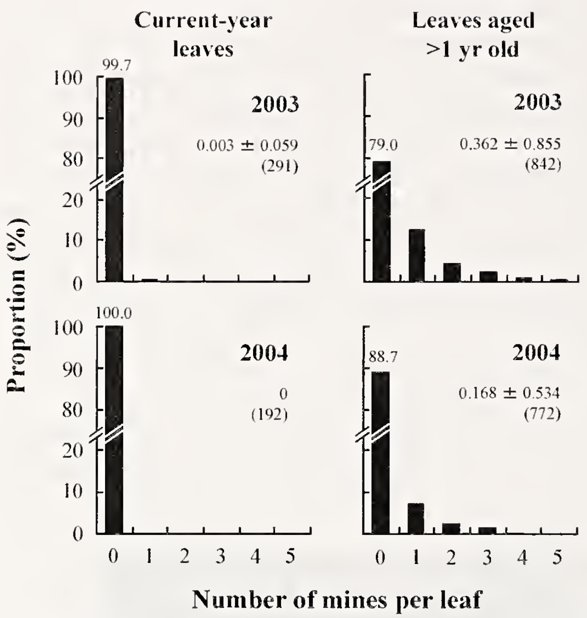


FIG. 2. Frequency distribution of *Coptotriche japoniella* mines on leaves newly expanded in the year and leaves aged 1 yr old or more in 2003 and 2004. Mean density per leaf is given with S.D. and sample size.

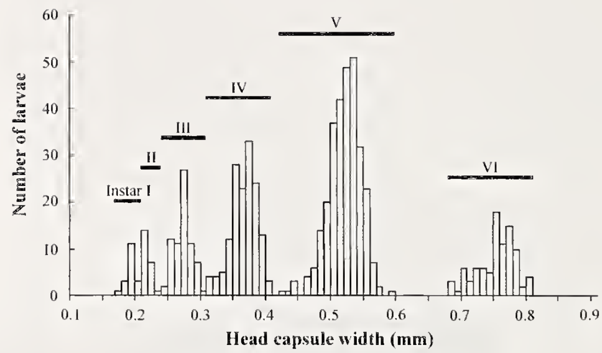


FIG. 3. Frequency distribution of head capsule width of *Coptotriche japoniella* larvae.

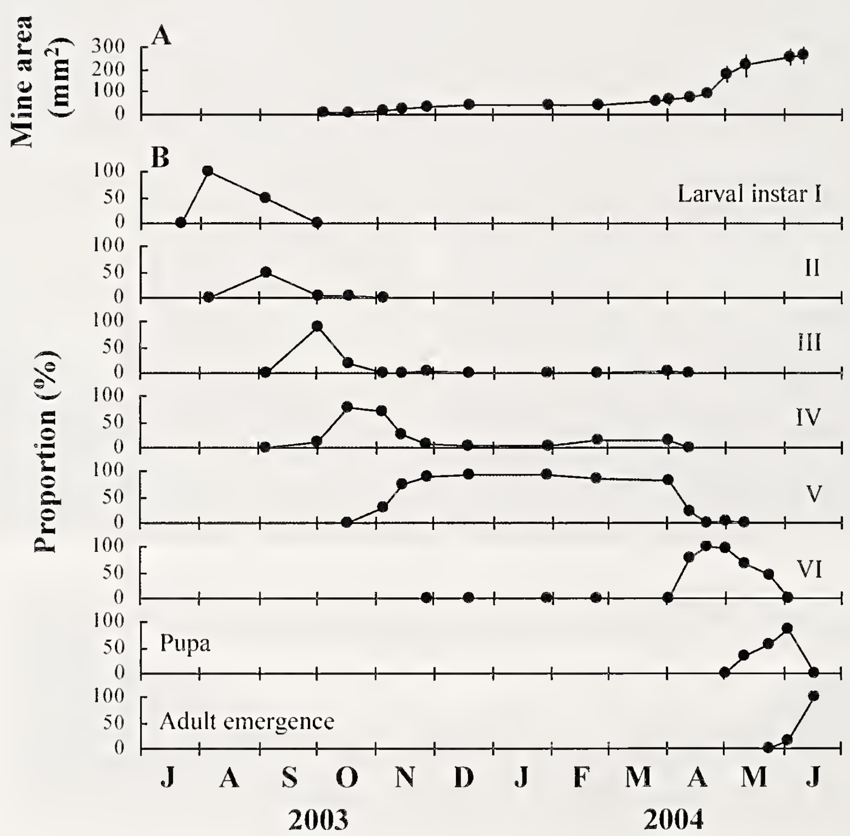


FIG. 4. Seasonal development of mines and immatures of *Coptotriche japoniella*. A, mean area of mines (± SD); B, frequencies of individuals in eight developmental stages.

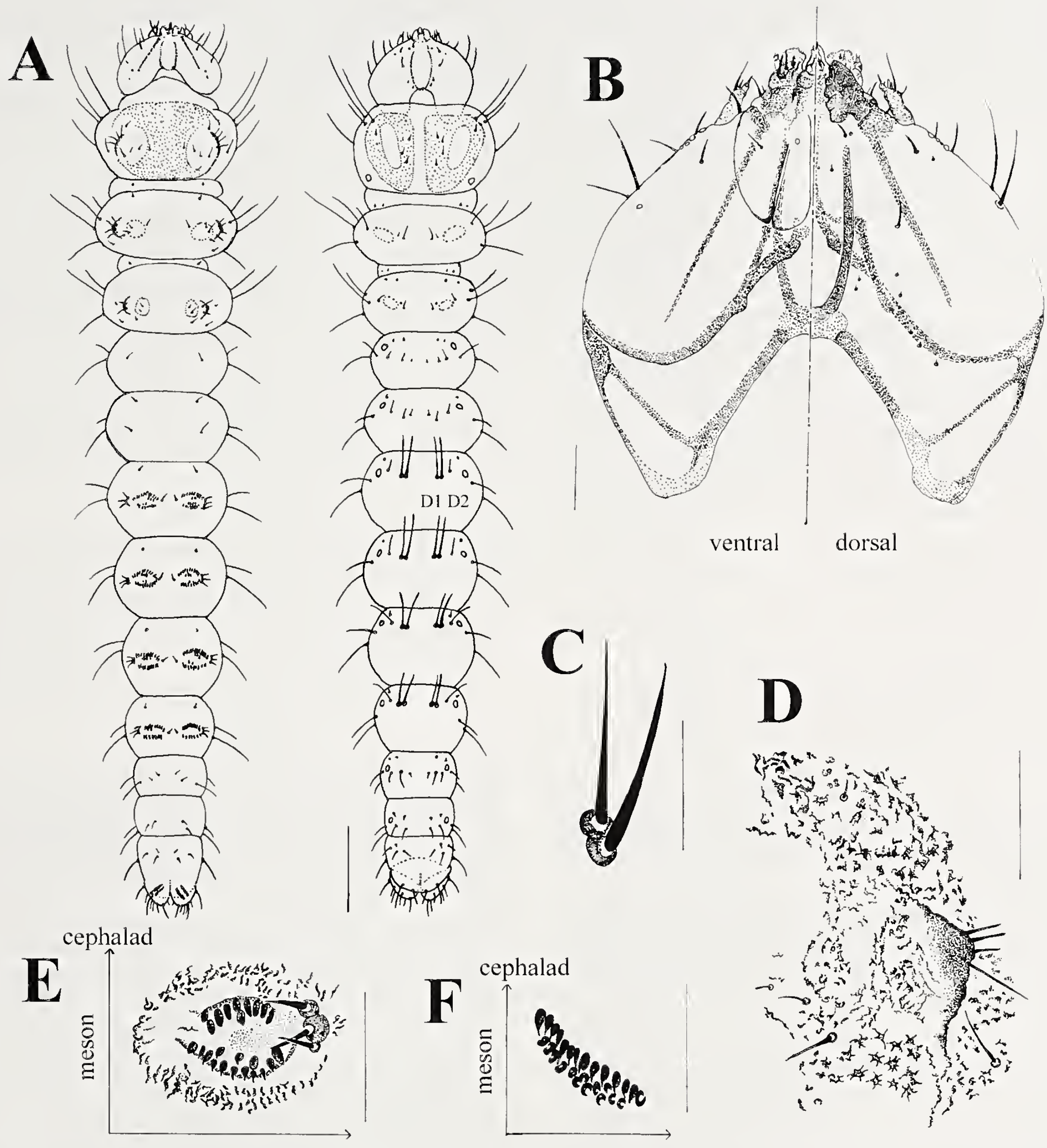


FIG. 5. Larval morphology of *C. japoniella*. **A,** ventral (left) and dorsal (right); **B,** head capsule (left: ventral, right: dorsal); **C,** D1 and D2 setae on 3rd abdominal segment; **D,** rudimentary leg on 1st thoracic segment; **E,** abdominal proleg with crochets on 5th abdominal segment; **F,** anal proleg with crochets. Bars indicate 0.1 mm.

only tischeriid besides *C. japoniella* to have such life history traits (Opler 1979).

Until now, 12 *Coptotriche* and 6 *Tischeria* species out of 114 tischeriids have been examined for both voltinism and host plants (Table 2). Three species with a facultatively bivoltine life cycle occur in Europe, showing univoltinism in the northern region and bivoltinism in the middle to southern region. The geographic variation in voltinism of these species is probably due to temperature conditions. Although *C. gaunacella* (Duponchel), which also occurs in northern to southern Europe, has been regarded as univoltine (Emmet 1976), it may be bivoltine in the southern region. Only *C. japoniella* and *C. discreta* are tischeriids that have a univoltine life cycle and are associated exclusively with evergreen plants in temperate regions.

TABLE 1. Voltinism and leaf type (i.e. evergreen and deciduous) of host plants of 12 *Coptotriche* and 6 *Tischeria* species.

Species	Voltinism	Host plants		References
		Evergreen	Deciduous	
Coptotriche discreta (Braun)	Univoltine	+		Opler (1979)
Coptotriche japoniella Puplesis & Diskus	Univoltine	+		Present study
Coptotriche gaunacella (Duponchel)	Univoltine		+	Emmet (1983)
Coptotriche angusticollella (Duponchel)	Facultatively bivoltine		+	Kuroko (1982), Emmet (1983)
Tischeria ekebladella (Bjerkander)	Facultatively bivoltine		+	Jordan (1995)
Tischeria dodonaea Stainton	Facultatively bivoltine		+	Emmet (1983), De Prins & Steeman (2007)
Coptotriche heinemanni (Wocke)	Bivoltine		+	Kuroko (1982)
Coptotriche marginea (Haworth)	Bivoltine		+	Emmet (1983)
Coptotriche malifoliella (Clemens)	Bivoltine		+	Braun (1972)
Coptotriche citrinipennella (Clemens)	Multivoltine		+	Braun (1972)
Coptotriche badiiella (Chambers)	Multivoltine		+	Braun (1972)
Coptotriche purinosella (Chambers)	Multivoltine		+	Braun (1972)
Coptotriche crataegifoliae (Braun)	Bivoltine		+	Braun (1972)
Tischeria decidua Wocke	Bivoltine		+	Teramoto (1996)
Tischeria quercifolia Kuroko	Bivoltine		+	Kuroko (1982)
Tischeria naraensis Sato	Bivoltine		+	Sato (unpublished)
Coptotriche consanguinea (Braun)	Multivoltine	+	+	Braun (1972)
Tischeria ceanothi Walsingham	Bivoltine	+	+	Fasoranti (1984)

On the whole, therefore, tischeriids depending on deciduous plants tend to be bi- or multivoltine, while those depending on evergreen plants tend to be univoltine.

The voltinism in tischeriids can relate to nutritional differences in foliage between deciduous and evergreen plants. Reich *et al.* (1998) reviewed published data, and demonstrated that leaves aged 1 yr or more have a smaller amount of nitrogen (15.0 ± 6.1 mg g^{-1} (mean ± SDs) for 27 species) than leaves of deciduous trees or current-year leaves of evergreen trees (22.2 ± 6.5 mg g^{-1}, for 91 species). Actually, 1 year old leaves of *E. japonica* contain as large an amount of nitrogen (15.2 ± 0.9 mg g^{-1}, n=10) as those of other evergreen trees (Oishi & Sato, unpublished data). In general, nitrogen contents greatly influence the growth performance of folivorous insect larvae (Schoonhoven *et al.* 1998; Chown & Nicolson 2004; Oishi & Sato 2006). If this is true for tischeriids, a smaller amount of nitrogen contents in evergreen leaves would have delayed larval development of the leafminers, resulting in the evolution of univoltine life cycles.

Larval morphology. Davis (1987) presented the following diagnostic characters of tischeriid larvae: a strongly depressed head, deep epicranial notch, four to six stemmata arranged in a horizontal line along the lateral edge of the head, setae D1 and D2 arising extremely close together on the 3rd to 6th abdominal segments, the absence of thoracic legs, and poorly developed ventral prolegs. As Fig. 5 shows, we recognized these charaeters except for stemmata in *C. japoniella*; the number of stemmata was four on each side of the head. In addition, we present rudimentary legs on the three thoracic segments as a diagnostic character (Fig. 5A, D); this eharacter has been found in other tischeriid species (Braun 1972; Davis 1987).

Davis (1987) also mentioned that crochets are usually present on the ventral prolegs, and arranged in multiserial bands or ineomplete ellipses. When Leraut (1993) erected a new genus *Emmetia* for species that were associated with Rosaseae, he indicated that larvae of the new genus possess crochets on the ventral prolegs, whereas those of *Tischeria* (in his sense) that are associated with Fagaceae lack them. However, he examined no tischeriids that are associated with Asteraceae or Malvaceae. Later Puplesis & Diškus (2003) classified those tischeriids into a new genus, *Astrotischeria*, and also synonymized *Emmetia* with *Coptotriche*, without referring to the crochets of the ventral prolegs. We confirmed the presence of crochets

on the ventral prolegs in a *Coptotriche* sp. that is associated with evergreen oaks (*Quercus* spp.) besides *C. japoniella* in Japan (Sato, unpublished), thus suggesting that the presence of crochets on the ventral prolegs is common to *Coptotriche*. In contrast, it seems that *Astrotischeria* larvae do not always possess crochets on the ventral prolegs. Braun (1972: fig. 22) clearly drew crochets on the ventral prolegs in the larva of *A. heliopsisella* (Chambers), whereas we found them in *Astrotischeria* sp. that were collected from *Montanoa hibiscifolia* (Benth.) (Asteraceae) in Costa Rica (Sato, unpublished). Taking it into account that crochets are often used as a diagnostic character for families and genera of Lepidoptera (Stehr 1987), the genus *Astrotischeria* might be possibly divided into two or more genera. Further studies of larval crochets, especially in *Astrotischeria*, should be undertaken.

ACKNOWLEDGEMENTS

We thank Dr. F. Komai for his valuable advice in the course of this study. Mr. K. Nishida was kind enough to provide us with adult and larval specimens of *Astrotischeria*. This study was supported financially by a Grant-in-Aid for Scientific Research (C) (No.16800017) from the Japan Society for the Promotion of Science.

LITERATURE CITED

BRAUN, A.F. 1972. Tischeriidae of America north of Mexico (Microlepidoptera). Mem. Am. Entomol. Soc. 28: i + 148 pp.

CHOWN, S.L. & S.W. NICOLSON. 2004. Insect physiological ecology. Oxford University Press, New York. 254 pp.

DAVIS, D.R. 1987. Tischeriidae (Tischerioidea). Pp. 354–357. *In* Stehr, F.W. (ed.), Immature Insects. Kendall/Hunt, Dubuque.

DE PRINS, W. & C. STEEMAN. 2007. Catalogue of the Lepidoptera of Belgium. (http://www.phegea.org/)

EMMET, A.M. 1976. Tiseheriidae. Pp. 272–276 in Heath, J. (ed.), The Moths and Butterflies of Great Britain and Ireland, Vol. 1. The Curwen Press, London.

FASORANTI, J.O. 1984. The life history and habits of a *Ceanothus* leaf miner, *Tischeria immaculata* (Lepidoptera: Tischeriidae). Can. Entomol. 116: 1441–1448.

HISAI, N. 1979. Preliminary report on the life history of the microlepidopterous leaf miners. Rept. Inst. Nat. Stu. 9: 25–32. (in Japanese with English abstract)

KUROKO, H. 1982. Tischeriidae. Pp. 58–59. *In* Inoue, H., S. Sugi, H. Kuroko, S. Moriuti & A. Kawabe, Moths of Japan, Vol.1. Kodansha, Tokyo, Japan.

JORDAN, T. 1995. Life history and parasitoid community of the oak-leaf-mining moth *Tischeria ekebladella* (Bjerkander, 1975) (Lep., Tischeriidae) in Northern Germany. J. Appl. Ent. 119: 447–454. (in German with English abstract)

KITAMURA, S. & G. MURATA. 1979. Colored illustrations of wood plants of Japan, Vol. 2. Hoikusha Publishing, Osaka, Japan. 545 pp. (in Japanese)

LERAUT, P. 1993. Création d'un nouveau genre de Tischeriidae (Lepidoptera). Ent. Gall. 4: 64–65. (in French)

NITTA, I. & M. OHSAWA. 1997. Leaf dynamics and shoot phenology of eleven warm-temperature evergreen broad-leaved trees near their northern limit in central Japan. Plant Ecol. 130: 71–88.

OISHI, M. & H. SATO. 2006. Japanese oak silkmoth feeding preference for and performanee on upper-crown and lower-crown leaves. Entomol. Sci. 9: 161–169.

_____ & _____. 2008. Guild structure and coexistence mechanisms in the parasitoid assemblage assoeiated with a leafminer, *Coptotriche japoniella* (Lepidoptera, Tischeriidae), on an evergreen tree, *Eurya japonica* (Theaceae). Environ. Ent. 37: 1231–1240.

OPLER, P.A. 1979. Biology, ecology, and host specificity of microlepidoptera associated with *Quercus agrifolia* (Fagaceae). University of California Publications in Entomology, 75. University of California Press, Berkeley and Los Angeles, California. v + 83 pp.

PUPLESIS, R. & A. DIŠKUS. 2003. The Nepticuloidea and Tischerioidea (Lepidoptera) – A global review, with strategic regional revisions. Lututė Publishers, Kaunas. 512 pp.

REICH, P.B., D.S. ELLSWORTH, & M.B. WALTERS. 1998. Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. Funct. Ecol. 12: 948–958.

SATO, H. 1990. Parasitoid eomplexes of lepidopteran leaf miners on oaks (*Quercus dentata* and *Quercus mongolica*) in Hokkaido, Japan. Ecol. Res. 5: 1–8.

SCHOONHOVEN, L.M., T. JERMY, & J.J.A. VAN LOON. 1998. Insect-plant biology. Chapman & Hall, London. 409 pp.

STEHR, F.W. 1987. Order Lepidoptera. Pp. 288–596. *In* Stehr, F. W. (ed.), Immature Insects. Kendall/Hunt, Dubuque.

TERAMOTO, N. 1996. Studies on Lepidopterous inseet fauna on Fagaceous plants, as the food plants of the wild silk moth, *Antheraea yamamai*. Spec. Bull. Shiga. Agric. Exp. Stn, 19. Shiga Prefectural Agricultural Experiment Station, Shiga, Japan. iv + 216pp. (in Japanese)

WALSINGHAM, L. 1890. Steps towards a revision of Chambers's index, with notes and descriptions of new species. Insect Life 2: 322–326.

YAMAMOTO, K. 1997. LIA for Windows 32, ver 0.376,1. (http://hp.vector.co.jp/authors/VA008416/index.html)

ZELLER, P.C. 1839. Versuch einer naturgemäßen Eintheilung der Schaben, Tinea. Isis Ency. Zeit. Oken, 32 (3): 167–220.

Received for publication 13 February; revised and accepted 13 November 2008.

Journal of the Lepidopterists' Society
63(2), 2009, 100-109

HEMARIS THETIS (BOISDUVAL, 1855) (SPHINGIDAE) IS A DISTINCT SPECIES

B. CHRISTIAN SCHMIDT

Canadian Food Inspection Agency, Canadian National Collection of Insects, Arachnids and Nematodes, K.W. Neatby Bldg., 960 Carling Ave., Ottawa, ON CANADA K1A 0C6; email: schmidtcb@inspection.gc.ca

ABSTRACT. Western North American populations previously treated as *Hemaris diffinis* (Boisduval) are shown to be a distinct species, *Hemaris thetis* (Boisduval), based on differences in habitus, genitalic morphology, mtDNA sequence variation and larval phenotype. Both species occur in strict sympatry at several localities in western Alberta without evidence of intergradation. *Hemaris senta* is a colour variant of *H. thetis*, and synonomized under the latter. Adults and diagnostic characters are illustrated, and the synonomy of *H. diffinis* is revised.

Additional key words: cryptic species, DNA barcoding, *Hemaris senta*, *Hemaris diffinis*.

The genus *Hemaris* Dalman (Sphingidae: Macroglossinae) currently contains 19 species (Kitching & Cadiou 2000), occurring primarily in temperate regions of the northern hemisphere. Four species are recognized in North America, namely *thysbe* (Fabricius, 1775), *gracilis* (Grote & Robinson, 1865), *senta* (Strecker, 1878), and *diffinis* (Boisduval, 1836) (Hodges 1971; Tuttle 2007). *Hemaris diffinis* and the taxa historically associated with it have long been a confusing lot, since there is little structural variation in genitalia (compared to congeners), with significant geographic and seasonal variation in phenotype. Here, I examine the morphological, ecological and molecular variation of western North American populations previously assigned to *H. diffinis*, with special emphasis on the contact zone between the Great Plains, Boreal and Cordilleran faunal regions in Alberta, Canada. These data show that two western species have gone under the name *H. diffinis*, and that *H. senta* is a color form of the second, unrecognized species, *H. thetis*.

Taxonomic history of *Hemaris diffinis*. The influential work of Abbot & Smith (1797) was apparently the first to illustrate *H. diffinis*, although referred to the European species *H. fuciformis* (L.) therein. Boisduval (1836) subsequently described and illustrated *diffinis*, and no other names for the *Hemaris diffinis* group were proposed until he described *thetis* two decades later (Boisduval 1855). As was often the case at that time, the provenance of the *diffinis* type material was vague, indicated only as "Amerique septentrionale". Comparison of the illustration accompanying the description, as well as the illustration in Abbot & Smith (1797), which Boisduval (1875) considered to be *diffinis*, suggests that the type of *diffinis* represents the large, dark phenotype typical of the southeastern US populations, a conclusion also reached by Rothschild & Jordan (1903). The most likely type locality is therefore the southeastern Atlantic seaboard, possibly Georgia. Type material of *diffinis* is extant in the Carnegie Museum of Natural History, Pittsburgh, PA (1. Kitching, pers. comm.).

Phenotypic variation among multiple annual generations, together with geographic variation, resulted in new names being proposed for various forms of *H. diffinis* (*sensu stricto*). Through rearing a second generation from known first generation females, Smyth (1900) showed that seasonal variation in phenotypes had resulted in erroneous recognition of separate species. Rothschild & Jordan's (1903) seminal revision reviewed the 13 *diffinis*-group taxa described to that point, and synonymized all but one under *diffinis*, based on perceived lack of diagnostic differences in male genitalia, and the phenotypic variation established to be seasonal by Smyth (1900). Rothschild & Jordan (1903) considered *H. thetis* (*sensu novo*, listed as *H. brucei* French by these authors) distinct from *diffinis*, based on the fact that it occurred in sympatry with *diffinis* and remained distinguishable from it. These authors segregated *diffinis* into three subspecies, *H. d. diffinis* (Atlantic region), *H. d. senta* (Great Plains) and *H. d. thetis* (Rocky Mountains westward). Although various nomenclature changes were implemented by subsequent authors (discussed below), the concept of a transcontinental species and a western species was followed by subsequent authors (Barnes & McDunnough 1910; Hodges 1971; Tuttle 2007).

In their checklist of the Sphingidae of North America, Barnes & McDunnough (1910) retained the species-level taxonomy of Rothschild & Jordan (1903), although revising the name *senta* as a senior synonym of *H. brucei*, and providing the name *ariadne* Barnes & McDunnough for the Great Plains *H. diffinis senta* of Rothschild & Jordan. They retained the geographic subspecific groupings of *diffinis*, but also recognized the taxon *aethra* (Strecker) in eastern North America (Ontario and Quebec) in addition to *H. d. diffinis*.

Fig. 1. Habitus of adult *H. thetis* (**A, B**) and western North American *H. diffinis* (**C**). The typical *thetis* phenotype is shown in (**A**) (AB: 15 km SW Beaver Mines, 23-v-99, B.C. Schmidt coll.), the "*senta*" phenotype in (**B**) (CO: 4 mi NW Boulder, 6900', 8-vi-61, W.R.M. Mason coll.), and typical Western *diffinis* (**C**) (SK: 13 KM NNE Eastend, 29-v-03, B.C. Schmidt coll.).

Subsequent faunal treatments have followed this species-level arrangement, i.e. with *H. diffinis* and *H. senta* as species, but without recognizing subspecies (Hodges 1971; Kitching & Cadiou 2000; Tuttle 2007). Bridges (1993) listed *thetis* as a subspecies of *diffinis*, but did not comment on the change in taxonomic status for *thetis*, and it was therefore again revised to synonymy under *diffinis* by Kitching & Cadiou (2000).

Methods and Materials

Specimens examined. The following abbreviations are used herein for specimen depositories:

CNC: Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario

CMNH: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania

CSU: C.P. Gillette Arthropod Biodiversity Museum, Colorado State University, Colorado

DEB: Private collection of Don. E. Bowman, Pueblo West, Colorado.

FMNH: Field Museum of Natural History, Chicago, Illinois

MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts

MNHN: Muséum National d'Histoire Naturelle, Paris

NHML: Natural History Museum, London

NMNH: National Museum of Natural History (formerly United States National Museum), Washington,. DC

UASM: University of Alberta Strickland Entomological Museum, Edmonton, Alberta

Approximately 750 specimens were examined in this study, primarily those of the CNC and UASM. Voucher specimen data for dissections and molecular analysis are given in Table 1. Data for molecular voucher specimens, including trace files and photographs, are available at http://barcodinglife.com (project: Lepidoptera: *Hemaris* under the "Published Projects" tab). Molecular sequences are deposited in GenBank, with accession numbers EU646618–EU646632. Distribution maps were compiled using DIVA-GIS 5.0. Geographic coordinates of collection localities were referenced using GEOLocate (Rios & Bart 2004), Placenames.com, and the Canadian Geographical Names Data Base (Natural Resources Canada 2006). Standard postal abbreviations for Canadian provinces and American states are used here.

Morphological techniques. Adult genitalia were prepared following the methods detailed by Lafontaine (2004). Cleaned, stained genitalia were stored and examined in 30% ethanol, and slide-mounted in Euparal before being photographed.

Molecular techniques. Specimens for molecular analysis were selected to maximize geographic coverage for western populations of *H. thetis* and *H. diffinis*, particularly for regions where the two taxa are sympatric. Specimens were also included from as near as practicable from the type localities of each taxon, namely north-central CA (*thetis*), central CO (*senta*) and GA (*diffinis*) (Table 1). Molecular variation was assessed based on the 658 bp 'barcode' region of the first subunit of the cytochrome oxidase (*cox1*) gene (Hebert *et al.* 2003), corresponding to nucleotide positions 1490–2198 of the *Drosophila yakuba* mitochondrial genome (Clary & Wolstenholme 1985). DNA was extracted from one leg removed from a dried specimen, sent to the University of Guelph in dry Eppendorf tubes, and processed as part of the "All Leps Barcode of Life Campaign" (www.lepbarcoding.org). DNA extraction, amplification and sequencing protocols for the Barcode of Life initiative are detailed in Hebert *et al.* (2003). Haplotypes of all *cox1* 'barcode' fragments were compared with phylograms constructed using the neighbor-joining method in PAUP 4.0*b10 (Altivec) (Swofford 2002). Phyletic distances were calculated using the Kimura-2-Parameter (K2P) distance model.

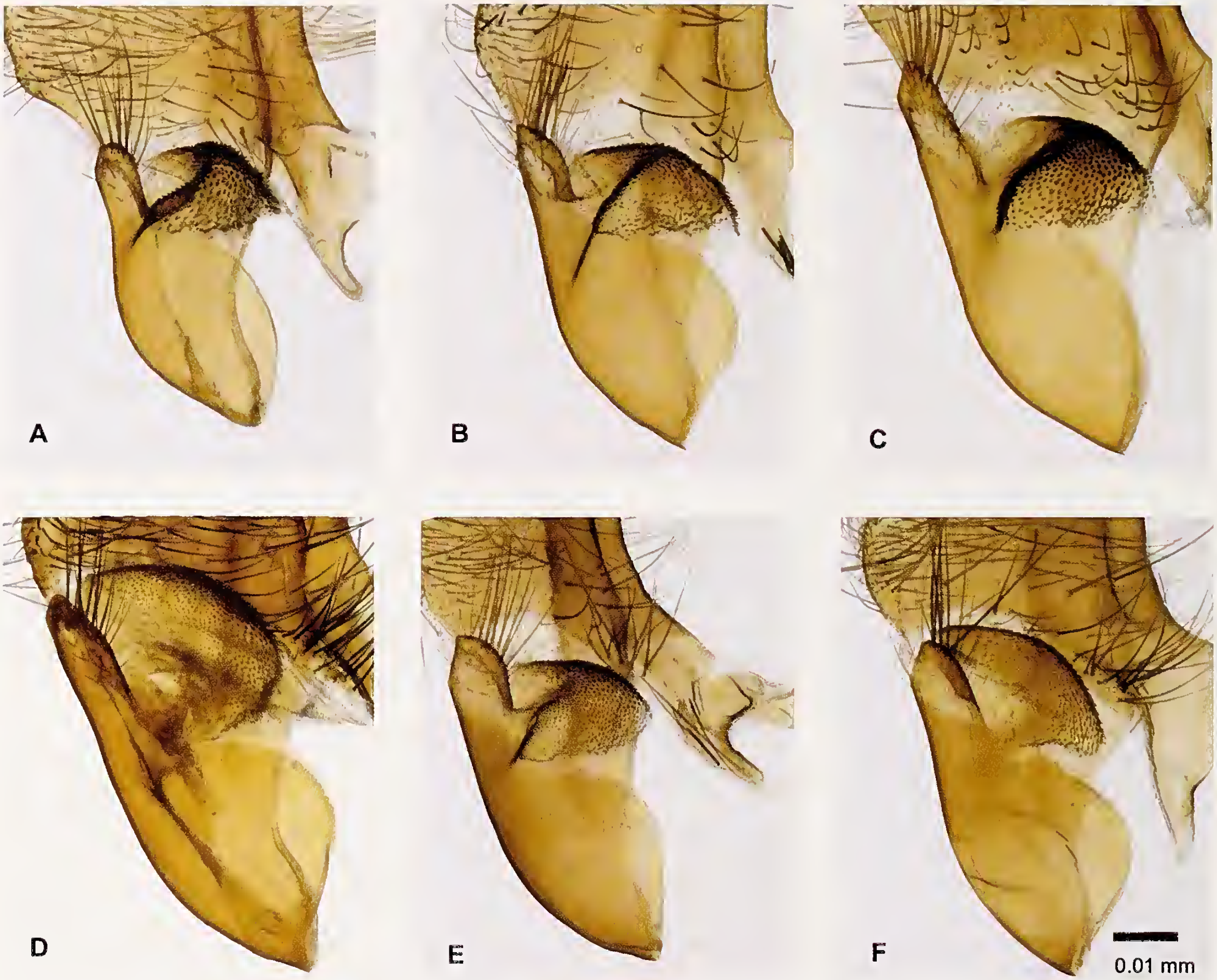


FIG. 2. Variation in structure of the left sacculus in *H. thetis* (top row) and *H. diffinis* (bottom row). Specimen data is given in Table 1 with corresponding dissection numbers: A) CNC13740, B) CNC12738, C) CNC13746, D) CNC13755, E) CNC13747, F) CNC13741.

RESULTS

Hemaris thetis (Boisduval, 1855) **Revised Status**

Macroglossa thetis Boisduval, 1855: 32.

Type material: two syntypes [AMNH?] *Type locality:* not stated, implied to be "Californie"; here restricted to Kelseyville, Sonoma Co., California. *Notes*. Most of the types of North American sphingid species described by Boisduval (1874) were purchased by Rothschild and were subsequently deposited in the Natural History Museum (London), then later purchased by B. P. Clark and so passed to the CMNH (I. Kitching, pers. comm.). The location of types for species described by Boisduval prior to 1875 is less clear, but a *thetis* syntype may also be at the CMNH. The second syntype (female) may be in the AMNH based on Grote's statement that "During our recent visit, Dr. Boisduval kindly communicated to us a specimen of *S. thetis* for the purpose of publishing the species..." (Grote & Robinson 1868: 325). As indicated by Boisduval (1855), the types of *thetis* were collected by Lorquin. Emmel *et al.* (1998) provide a detailed summary of Lorquin's collecting itinerary, and conclude that he collected in (at least) Sonoma, Marin, Placer, and El Dorado counties of northern California prior to 1855. The type locality of *thetis* is therefore restricted to Kelseyville, Sonoma Co., California, where this species is known to occur.

Hemaris palpalis Grote, 1874: 145. **Revised Synonomy**

Type material: holotype, presumably a male [MCZ]. *Type locality:* restricted to "Gilroy, Santa Clara County, California; about 80 miles south of San Francisco." by Grote (1875: 224). *Notes*. In the original description Grote (1874) states that the type was labelled "with the ticket "Gilroy", by the late G. R. Crotch, in British Columbia...", subsequently corrected to Gilroy, California (Grote 1875), as also noted by Edwards (1875). *Hemaris palpalis* was described with "bright orange" palps, which in all likelihood was due to pollen accumulation on the palps, as noted by Rothschild & Jordan (1903).

Hemaris rubens H. Edwards, 1875: 88. **Revised Synonomy**

Type material: two syntypes, sex not stated [AMNH?]. *Type locality:* "Oregon...; Lake Tahoe, Cal." *Notes*. Edwards differen-

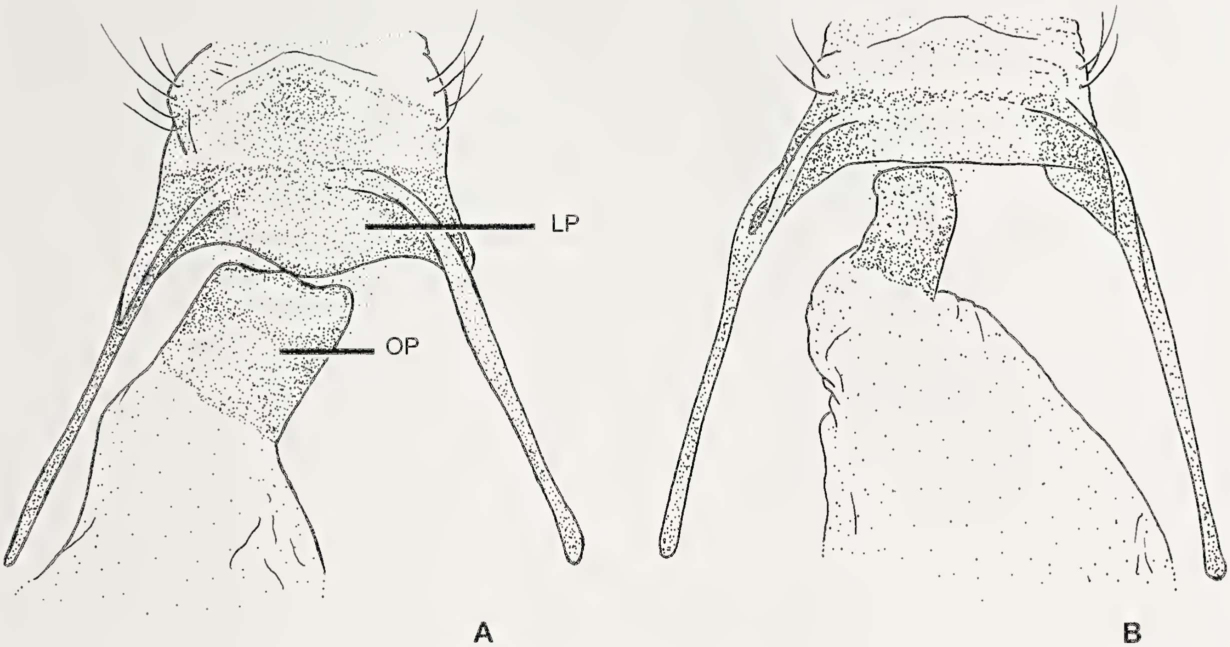


FIG. 3. Lamella postvaginalis (LP) and sclerotized ostial plate (OP) of female *H. thetis* (left) and *H. diffinis* (right).

tiated this taxon from his concept of *thetis* based on more reddish wing markings and more extensive yellow dorsal abdominal vestiture.

Hemaris cynoglossum H. Edwards, 1875: 88. **Revised Synonomy**

Type material: two male and two female syntypes [AMNH?]. *Type locality:* "Napa County; Big Trees, Calaveras County, Cal.; Vancouver Island." *Notes.* Edwards (1875) described *cynoglossum* with the "thorax bright greenish olive, without the brownish tint observed in *thetis*". Edwards' concept of *thetis* appears to have been of the summer-flying, more orange colored *thetis* populations of southern California.

Macroglossa senta Strecker, 1878: 1858, pl. 2, f. 1. **Revised Status**

Type material: holotype [FMNH?] *Type locality:* Tierra Amarilla, New Mexico. *Notes*. Distinguished based on entirely yellow ventral thorax and abdomen (excluding anal tuft), and wider ductus bursae of female genitalia (Hodges 1971). Examination of *senta* phenotypes from CO, UT, and CA confirms the genitalic differences between *senta* and *diffinis*, and shows that *senta* is structurally indistinguishable from *thetis*. Comparison of long series of southern BC specimens shows that the extent of ventral yellow vestiture varies somewhat, with specimens from hotter, drier habitats tending to show more yellow on abdominal segments 5 to 7 (some of these specimens, from Kaslo, BC were reported as *senta* by Hodges (1971)). Specimens from the east slope of the Sierra Nevada in California (Sonora Pass, Alpine Co.; also localities cited by Tuttle [2007]) tend to be more yellow dorsally like *senta*, but lack the continuous yellow ventrum. Leg vestiture shows similar variation in extent of yellow scaling; for example, *cynoglossum* was described based in part on the black rather than yellow hind-tibiae. The consistency of the diagnostic genitalic and larval characters discussed below, across western populations varying from *senta* to *thetis* phenotypes, leads me to conclude that *senta* and *thetis* represent a single species, with *thetis* as the oldest name.

Hemaris brucei French, 1890: 133. **Revised Synonomy**

Type material: single male [destroyed?]. *Type locality:* "Colorado". *Notes*. Barnes & McDunnough (1910) indicated that the type was destroyed by dermestids. However, there is a specimen of *brucei* labelled "type" in the USNM, the true status of which remains to be determined (I. Kitching, pers. comm.). French's material in the Illinois Natural History Survey should also be examined.

Hemaris minima Frankenbusch, 1925: 90. **Revised Synonomy**

Type material: described from a single specimen, sex not stated [type depository unknown]. *Type locality:* implied to be Palaearctic in original description [erroneous]. *Notes*. As discussed by Kitching & Cadiou (2000), the type locality is incorrect, since Bang-Haas (1927) examined the type of minima and recognized it as the same taxon as "*senta*". Frankenbusch described minima as having a black ventral abdomen, not yellow as in the *senta* form.

Hemaris diffinis jordani Barnes & Benjamin, 1927: 51. **Revised Synonomy**

Type material: holotype male, allotype female, 36 male and four female paratypes [NMNH]. *Type locality:* "Southern Utah". *Notes*. A junior secondary homonym of *Haemorhagia fuciformis jordani* Clark, 1927; Eitschberger, Danner & Surholt (1996) provided the replacement name *heppneri*.

‡ *Haemorrhagia diffinis thetis f. mcdunnoughi* Clark, 1927: 104. **Revised Synonomy**

Notes. Unavailable infrasubspecific name. Described based on 10 specimens from "Senator Mts., [Bradshaw Mtns.] Arizona, ...Cochise Co., Arizona,...Pinal Mts., Gila Co., Arizona,...southern Utah,...Congress, Arizona,...White Mts., Utah." (Clark 1927).

Hemaris diffinis heppneri Eitschberger, Danner & Surholt, 1996 **Revised Synonomy**

Type material: holotype male, allotype female, 36 male and four female paratypes [NMNH]. *Type locality:* "Southern Utah". *Notes*. Proposed as a replacement name for *Hemaris diffinis jordani* Barnes & Benjamin, 1927.

Diagnosis. *Habitus.* Although there is some geographic variation in the extent of yellow vestiture on the thorax and abdomen, *thetis* can be reliably separated from *diffinis* where the two are sympatric or parapatric based on the following traits (Figure 1): The central anal tuft is black or black with some dorsal yellowish hairs (*senta* phenotypes, Fig. 1b), never solid yellow as in *diffinis* (Fig. 1c); The dorsal thorax and basal abdominal segments are evenly olive-coloured, not orange-yellow with pale yellow subdorsal hairs (giving a striped appearance) as in *diffinis*; subdorsal yellow stripe not extending through 4th abdominal segment (yellow subdorsal stripe extending through 4th segment in *diffinis*). These traits remained constant in all material examined from geographic areas where *thetis* and *diffinis* occurred together (central and southwestern AB; central CO), and specimens could be easily assigned to one of the two species based on color pattern. As discussed above under *senta*, ventral color is variable in *thetis* and is not a reliable diagnostic trait. The specimen illustrated as *H. senta* in Tuttle (2007: Plate 5 Fig. 18) is actually *H. diffinis*.

Genitalia. The most pronounced structural differences are in the female genitalia. The lamella postvaginalis forms a broader band, and the ridges forming the origins of the anterior apophyses are more strongly tapered caudally in *thetis*; the lamella postvaginalis also has a pronounced median lobe on the proximal margin, absent in *diffinis* (Fig. 2). The dorsal sclerotized plate of the ductus bursae is on average wider in *thetis* compared to *diffinis*, the width being about 1–1.2X that of the plate length, compared to 0.5–0.7X in *diffinis* (Fig. 2). The male genitalia are more variable, but the following subtle differences are evident: overall, the saccular region has a smoother (more finely scobinate) more elongate appearance in *thetis* than *diffinis*, with the scobinate, inner base flattened or convex, not curved and ridge-like as in *diffinis* (Fig. 3); the left saccular extension is on average shorter, more triangular, and broader-based (Fig. 3).

Larva and pupa. Tuttle (2007) provides an excellent summary of the larval differences between *thetis* (as western *diffinis* and *senta*) and *diffinis*, and the following is based largely on the description given therein: caudal horn short and stout, purplish in color and lacking a yellow base, curving caudad; spiracles orange. In *diffinis*, the horn is longer, black with a bright yellow base, and straight or curved cephalad, and the spiracles are black. Based on the few examples of pupal cases available to me (two *thetis* and three *diffinis*), the cremaster of *thetis* has a slightly broader base with a rounded taper towards the apex, compared to a straight taper in *diffinis*, giving the overall appearance of a more robust cremaster in *thetis*. More pupae should be examined to assess the variability of this trait.

Molecular variation. Nine *H. thetis* specimens were sequenced from southern British Columbia, southwestern and central Alberta, California, and Colorado, and compared to ten *diffinis* sequences from southeastern Alberta, southwestern Saskatchewan, Oklahoma, and Georgia (Table 1). *Hemaris thetis* samples consisted of three haplotypes, with six haplotypes for the *diffinis* samples (Fig. 4). Specimens from areas of sympatry identified as *H. thetis* based on color pattern exhibited "*thetis*" haplotypes (voucher numbers CNCNoctuoidea13841, CNCNoctuoidea13842, UASM58223, UASM58404; Table 1, Figure 1), as did the nominate *thetis* specimen from CA and *senta* from CO (Table 1; Figure 1). Although *diffinis* specimens from the immediate areas of sympatry (dissection numbers CNC13736, CNC13744, CNC13745; Table 1) were too old for molecular analysis, those from nearby sites expressed "diffinis" haplotypes (e.g. UASM99164, UASM99165; Table 1).

Divergence rates between *thetis* and *diffinis* ranged from 2.0% to 3.3% averaging 2.8%. A single sequence of *H. gracilis* was included for comparison, which differed from *thetis* and *diffinis* by averages of 7.9% and 8.4%, respectively. Divergence rates between *thetis* and *diffinis* are slightly higher than those observed in other Macroglossinae, i.e. members of the *Hyles euphorbiae* (L.) complex where Hundsdoerfer *et al.* (2005) observed interspecific divergence rates of 0.1–2.1% (uncorrected pairwise distances, *cox1-2* genes). Additional geographic and molecular sampling of the *Hemaris diffinis* group should be carried out to confirm if the variation of the *cox1* gene is fully congruent with the non-molecular characters that distinguish *Hemaris thetis*.

Biology. Typical of the genus, *H. thetis* is diurnal and hovers at flowers to take nectar. I have found yellow spring-blooming flowers to be especially productive for finding *thetis*, such as dandelion (*Taraxacum officinale* Wigg.) (Asteraceae), early yellow locoweed (*Oxytropis*

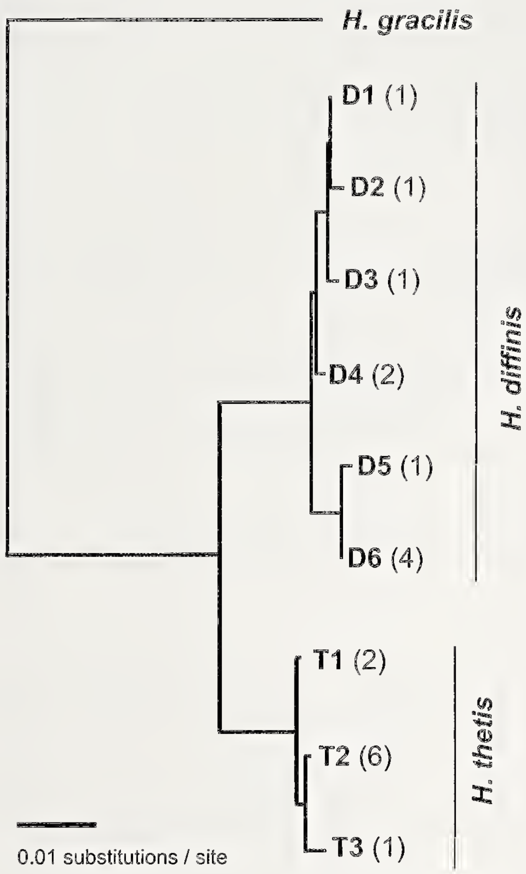


FIG. 4. Neighbor-joining tree of *Hemaris* haplotypes, based on the 658 base-pair barcode fragment of the mtDNA gene *cox1*. Haplotypes correspond to those given in Table 1, with number of individuals sharing a haplotype given in brackets.

FIG. 5. Distribution of examined specimens of *H. thetis* (black) and western North American *H. diffinis* (white). Half-filled circles indicate records of both species at the same site (Alberta), or adjacent sites too close to map separately (Colorado).

sericea Nutt.) (Fabaceae) and also stickseed (*Hackelia* Boraginaceae sp.) and ornamental sour cherry (*Prunus cerasus* L.) (Rosaceae). Larval hosts consist of members of the Caprifoliaceae, but specific host species for *thetis* should be re-assessed in light of the confusion with *diffinis*. Snowberry (*Symphoricarpos* species, Caprifoliaceae) is undoubtedly referable to *thetis* (host records for *senta*, (Tuttle 2007); also reared CNC specimens). A female *thetis* (voucher # CNC_13759, Table 1) collected in boreal forest habitat was displaying oviposition flight behavior around *Lonicera involucrata* Rich., another probable host. Jones (1951) indicated "creeping snowberry" as a host in BC, which is unusual since this is not a true snowberry but a species of Ericaeeae, *Gaultheria hispidula* (L.). This could be dismissed as an erroneous record, yet a reared BC *thetis* specimen from a larval collection on "*Chiogenes* sp." (1956; CNC) points to the same host, since *G. hispidula* is the only native BC species that was previously placed in *Chiogenes*. This plant inhabits wet, boggy areas – perhaps boreal populations of *thetis* utilize ericaceous hosts (which are also used by *H. gracilis* [Tuttle 2007]). Another odd host record requires comment: Abbot & Smith (1797) describe (and illustrate) the larvae feeding on *Amsonia tabernaemontana* Walt. (Apocynaceae), and Rothschild & Jordan (1903) indicate *Apocynum* (Apocynaceae) as a host. Plants of the Apocynaceae are well-known for their latex production and toxic properties, and use of these plants by *diffinis* should be investigated.

Hemaris thetis has a single annual flight throughout most of the northern parts of its range, with a second flight in the south Okanagan valley of BC (and likely southwards), as indicated by late May/early June and early to mid-July collection dates. Late June records are from higher elevations or latitudes, suggesting an extended or later spring flight, not a second brood. *Hemaris diffinis* is generally found in warmer, drier

Table 1. Specimen data for molecular and dissection voucher specimens.

Species	Country	Province	Locality	Latitude	Longitude	Date	Collector	Depository	Sex	Disection #	DNA voucher #	GenBank #	Haplotype
Hemaris diffinis	CAN	AB	Edmonton	53.55	-113.47	5-May-42	Bowman, K.	CNC	m	CNC_13736	-	-	-
Hemaris diffinis	CAN	AB	Elkwater Park	49.66	-110.28	5-Jun-52	Konotopetz, L.A.	CNC	m	CNC_13752	-	-	-
Hemaris diffinis	CAN	AB	Fort McMurray	56.73	-111.38	6-Jun-63	Brown, W.J.	CNC	f	CNC_13762	-	-	-
Hemaris diffinis	CAN	AB	Lethbridge	49.70	-112.82	6-Jun-29	Pepper, J.H.	CNC	f	CNC_13737	-	-	-
Hemaris diffinis	CAN	AB	Waterton Lakes NP, Rowe L. trail, 5500' - 6500'	49.05	-114.00	17-Jun-61	Milliron, H.E.	CNC	f	CNC_13744	-	-	-
Hemaris diffinis	CAN	AB	Red Deer River, 10km N Jenner	50.83	-111.16	19-May-00	Schmidt, B.C.	CNC	m	-	CNCNoctuoidea 13840	EU646623	D6
Hemaris diffinis	CAN	AB	Grande Prairie region, Kleskun Hill	55.25	-118.53	3-Jun-00	Schmidt, B.C.	UASM	m	-	UASM58219	EU646618	D6
Hemaris diffinis	CAN	AB	Grande Prairie region, Kleskun Hill	55.25	-118.53	3-Jun-00	Schmidt, B.C.	UASM	m	-	UASM58222	EU646619	D6
Hemaris diffinis	CAN	AB	Jenner, 10 km N	50.83	-111.16	3-Jun-04	Schmidt, B.C.	UASM	m	-	UASM99164	EU646621	D6
Hemaris diffinis	CAN	AB	Grande Prairie region, Kleskun Hill	55.25	-118.53	3-Jun-00	Schmidt, B.C.	UASM	m	-	UASM58220	EU646620	D5
Hemaris diffinis	CAN	AB	Jenner, 10 km N	50.83	-111.16	3-Jun-04	Schmidt, B.C.	UASM	m	-	UASM99165	EU646622	D1
Hemaris diffinis	CAN	AB	Red Deer River, 10km N Jenner	50.83	-111.16	19-May-00	Schmidt, B.C.	CNC	m	-	LEP041271	-	D4
Hemaris diffinis	CAN	MB	Miniota	50.13	-101.03	10-Jun-37		CNC	f	CNC_13763	-	-	-
Hemaris diffinis	CAN	MB	Norway House	53.99	-97.82	24-Jun-38	Brown, W.J.	CNC	f	CNC_13757	-	-	-
Hemaris diffinis	CAN	MB	Riding Mountain NP, Gorge Ck.	50.88	-100.25	25-Jun-79	Miller, S.J.	CNC	m	CNC_13760	-	-	-
Hemaris diffinis	CAN	NT	Fort Smith	60.04	-111.96	22-Jun-50		CNC	m	CNC_13751	-	-	-
Hemaris diffinis	CAN	ON	Constance Bay	45.49	-76.08	14-May-42	Freeman, T.N.	CNC	m	CNC_13746	-	-	-
Hemaris diffinis	CAN	ON	Manitoulin Dist., Misery Bay	45.79	-82.73	15-Jun-96	Morton, J.	CNC	m	CNC_13753	-	-	-
Hemaris diffinis	CAN	ON	Marmora	44.48	-77.68	10-May-52	Vockeroth, J.R.	CNC	f	CNC_13767	-	-	-
Hemaris diffinis	CAN	ON	Nipigon	49.01	-88.27	11-Jul-07	Fletcher, J.	CNC	f	CNC_13761	-	-	-
Hemaris diffinis	CAN	SK	Eaglehill Ck.	52.35	-108.97	18-May-69	Brooks, A.R.	CNC	m	CNC_13739	-	-	-
Hemaris diffinis	CAN	SK	Harlan	53.60	-109.92	11-Jun-47	Bruggeman, P.F.	CNC	m	CNC_13738	-	-	-
Hemaris diffinis	CAN	SK	Storthoaks	49.38	-101.60	14-Apr-05	Noble, T.M.	CNC	m	CNC_13740	-	-	-
Hemaris diffinis	CAN	SK	13 km NNE Eastend, Pine Cree Campground	49.62	-108.76	29-May-03	Schmidt, B.C.	CNC		-	CNCNoctuoidea 13846	EU646624	D4

Table 1. Continued on next page

Table 1. Continued

Species	Country	Province	Locality	Latitude	Longitude	Date	Collector	Depository	Sex	Disection #	DNA voucher #	GenBank #	Haplotype
Hemaris diffinis	USA	CO	Boulder, 4.5 mi N, 5500'	40.08	-105.27	19-Jun-61	Stainer, J.R.	CNC	m	CNC_13745	-	-	-
Hemaris diffinis	USA	GA	Cordon Co., Calhoun	34.50	-84.95	14-Sep-07	Adams, J.K.	CNC	m	-	LEP041279	-	D2
Hemaris diffinis	USA	OK	Comanche Co., Fort Sill	34.67	-98.38	26-Jul-03	Carhart, M.C.	CSU	m	-	NOC14993	-	D3
Hemaris gracilis	CAN	AB	Richardson Dunes Wild. Pk.	58.21	-111.39	14-Jun-00	Schmidt, B.C.	UASM	f	-	UASM19688	EU646625	-
Hemaris thetis	CAN	AB	Calgary, Head of Pine Ck.	50.86	-114.22	18-Jun-14	Dod, F.H.W.	CNC	m	CNC_13734	-	-	-
Hemaris thetis	CAN	AB	Crowsnest Pass	49.63	-114.63	7-Jun-40	Pepper, J.H.	CNC	f	CNC_13735	-	-	-
Hemaris thetis	CAN	AB	Waterton Lakes	49.05	-113.91	18-Jun-56	Sterns, E.E.	CNC	m	CNC_13741	-	-	-
Hemaris thetis	CAN	AB	Waterton Lakes	49.05	-113.91	18-Jun-56	Sterns, E.E.	CNC	m	CNC_13742	-	-	-
Hemaris thetis	CAN	AB	Waterton Lakes	49.05	-113.91	18-Jun-56	Sterns, E.E.	CNC	m	CNC_13743	-	-	-
Hemaris thetis	CAN	AB	Opal Natural Area	54.01	-113.27	5-Jun-03	Schmidt, B.C.	CNC	f	CNC_13759	CNCNoctuoidea 13841	EU646630	T1
Hemaris thetis	CAN	AB	West Castle R. Road, 15km SW Beaver Mines	49.38	-114.37	22-May-99	Schmidt, B.C.	CNC	m	-	CNCNoctuoidea 13842	EU646631	T2
Hemaris thetis	CAN	AB	Beaver Mines, 15 km W	49.34	-114.42	22-May-99	Anweiler, G.C.	UASM	m	-	UASM58223	EU646627	T2
Hemaris thetis	CAN	AB	Beaver Mines, 15 km W	49.34	-114.42	22-May-99	Anweiler, C.G.	UASM	m	-	UASM58404	EU646626	T2
Hemaris thetis	CAN	BC	Summerland	49.61	-119.68	26-May-90	Troubridge, J.	CNC	m	CNC_13754	-	-	-
Hemaris thetis	CAN	BC	Riondel, 2km S	49.76	-116.85	24-May-02	Schmidt, B.C.	CNC	m	-	CNCNoctuoidea 13843	EU646632	T2
Hemaris thetis	CAN	BC	Riondel, 2km S	49.76	-116.85	17-May-04	Schmidt, B.C.	UASM	m	-	UASM99166	EU646628	T2
Hemaris thetis	CAN	BC	Riondel, 2km S	49.76	-116.85	17-May-04	Schmidt, B.C.	UASM	m	-	UASM99167	EU646629	T2
Hemaris thetis	USA	AZ	Cochise Co.			1-Jul-26		CNC	f	CNC_13765	-	-	-
Hemaris thetis	USA	CA	Clendora	34.14	-117.86	31-Jul-35		CNC	m	CNC_13756	-	-	-
Hemaris thetis	USA	CA	Lake Co., Kelseyville	38.98	-122.84	20-Jun-38	Macheboeuf, C.	CNC	f	CNC_13766	-	-	-
Hemaris thetis	USA	CA	El Dorado Co., Ceorgetown	38.91	-120.84	31-Jul-06	Robinson, P.	CSU	f	-	NOC14990	-	T3
Hemaris thetis	USA	CO	Boulder, 4 mi NW 6900'	40.06	-105.32	17-Jun-61	Mann, C.H.	CNC	m	CNC_13747	-	-	-
Hemaris thetis	USA	CO	Boulder, 4 mi NW 6900'	40.06	-105.32	8-Jun-61	Mann, C.H.	CNC	m	CNC_13748	-	-	-
Hemaris thetis	USA	CO	Boulder, 4 mi NW 6900'	40.06	-105.32	17-Jun-61	Mann, C.H.	CNC	f	CNC_13749	-	-	-
Hemaris thetis	USA	CO	Boulder, 4 mi NW 6900'	40.06	-105.32	17-Jun-61	Mann, C.H.	CNC	f	CNC_13750	-	-	-
Hemaris thetis	USA	CO	Crand Co., Maryvale	39.93	-105.79	28-May-02	Bowman, D.E.	DEB	m	-	LEP041991	-	T1
Hemaris thetis	USA	WA	Belfast	48.55	-122.34	22-May-49	Frechin, D.P.	CNC	f	CNC_13758	-	-	-
Hemaris thetis	USA	WA	Tenino [Thurston Co.]	46.86	-122.85	30-May-51	Frechin, D.P.	CNC	m	CNC_13755	-	-	-

habitats, and is at least occasionally bivoltine (flying in May to early June and again in late July to August) as far north as the Peace River grasslands at the northwestern periphery of its range.

Distribution. Localities for examined specimens of *thetis* ranged from the west-central BC coast to southern CA and AZ, west to central AB and CO (Fig. 5). Alaskan populations (Tuttle 2007) are likely referable to *thetis*, but this requires confirmation. By comparison, *H. diffinis* is largely a Great Plains species, occurring northward in the western boreal region in more xeric habitats, such as the Peace River grasslands in northwestern AB (Fig. 5). *Hemaris diffinis* appears to be absent west of the continental divide. Both species occur together in the boreal region of central AB, and along the Rocky Mountain foothills. In the southern portion of the AB Rocky Mountains, where prairie and foothills habitats are juxtaposed at low elevations, the two can occur in strict sympatry; both species are represented in series of specimens from Waterton Lakes and Pine Creek (west of Calgary), AB (CNC), without evidence of intermediate phenotypes.

Discussion

The degree of seasonal variation exhibited by *H. thetis* appears to vary geographically. Summer-generation specimens from southern BC are not distinguishable from those of the spring generation, although July specimens from southern CA and AZ are larger and more yellow in color than the typical olive-yellow northern *thetis*. Structurally, these southern, summer *thetis* are identical to northern populations (and AZ *thetis* larvae are like those of the Pacific Northwest [Tuttle 2007]), so there is currently no reason to suspect that more than one species is involved. Documenting seasonal variation and voltinism throughout the range of *thetis* would shed additional light on these variation patterns. In a pattern parallel to that in *thetis*, summer generation *diffinis* from the northwestern parts of the range vary only slightly from the spring phenotype, where summer phenotypes are slightly more orange-yellowish overall. This contrasts sharply with the substantial seasonal variation in vestiture color and width/shape of the forewing marginal band seen in eastern *diffinis* populations (Smyth 1900). The Eastern 'subspecies' of *Hemaris diffinis* recognized long ago by Rothschild & Jordan (1903) and Barnes & McDunnough (1910), may warrant another closer look.

Acknowledgements

I thank Jocelyn Gill for providing technical assistance, and Gary Anweiler, Don Bowman, Boris Kondratieff, Doug Macaulay and Paul Opler for providing additional data and/or specimens. I am grateful to two anonymous reviewers and Ian Kitching who kindly provided a careful critique of this manuscript, and also provided valuable information on *Hemaris* type specimens.

Literature Cited

Abbot, J. & J.E. Smith. 1797. The natural history of the rarer lepidopterous insects of Georgia. Collected from the observations of Mr. John Abbot many years resident of that country by James Edward Smith. London: T. Bensley. Pp. 1–102.

Bang-Haas, O. 1927. Horae Macrolepidopterologicae Regionis Palaearcticae. Vol. 1. Dresden, Germany. 128 pp.

Barnes, W.M. & F.H. Benjamin. 1927. A new race of *Hemaris diffinis* (Lepid., Sphingidae). Bull. S. Calif. Acad. Sci. 26:51.

_____ & J. McDunnough. 1910. List of Sphingidae of America North of Mexico. Psyche 17:190–205.

Boisduval, J.B.A. 1836. *In*: [Roret, Suites à Buffon] Histoire naturelle des insectes. Species général des Lépidoptères. Volume 1. Paris: Librairie Encyclopédique de Roret. 690 pp.

_____. 1855. [Descriptions of Lepidoptera]. Bull. Soc. Ent. Fr. 3:32.

_____. [1875] 1874. Sphingides, Sesiides, Castnides. In: J.B.A. Boisduval & A. Guenée (eds.). Histoire naturelle des insectes. Species général des Lépidoptères Hétérocères. Volume 1. Paris: Librairie Encyclopédique de Roret, Pp. 1–568.

Bridges, C.A. 1993. Catalogue of the family-group, genus-group and species-group names of the Sphingidae of the world. C.A. Bridges, Urbana, Ill.

Clark, B.P. 1927. Descriptions of twelve new Sphingidae and remarks upon two other species. Proc. New England Zool. Cl. 9: 99–109.

Clary, D., & D.R. Wolstenholme. 1985. The mitochondrial DNA molecule of *Drosophila yakuba*: nucleotide sequence, gene organization and genetic code. J. Molec. Evol. 22:252–271.

Edwards, H. 1875. Pacific coast Lepidoptera. – No. 11. List of the Sphingidae of California and adjacent districts, with descriptions of new species. Proc. Calif. Acad. Sci. 6: 86–95.

Eitschberger, U., F. Danner, & B. Surholt. 1996. *Hemaris diffinis* heppneri nom. nov. pro *Hemaris diffinis* jordani Barnes & Benjamin, 1927 (Lepidoptera, Sphingidae). Atalanta 27:333.

Emmel, J.F., T.C. Emmel, & S.O. Mattoon. 1998. The types of California butterflies named by Jean Alphonse Boisduval: designation of lectotypes and a neotype, and fixation of type localities. Pp. 3–76. *In* T.C. Emmel (ed.), Systematics of western North American butterflies. Gainesville, FL, Mariposa Press. 878 pp.

Frankenbusch. 1925. *Hemaris* Aberr. Entomologische Zeitschrift. 38: 90.

French, G.H. 1890. Some new moths. Can. Ent. 22:133–135.

Grote, A.R. 1874. Notes on American Lepidoptera with descriptions of twenty-one new species. Bull. Buffalo Soc. Nat. Sci. 2:145–163.

_____. 1875. Check List of North American Sphinges. Bull. Buffalo Soc. Nat. Sci. 2:224–228.

_____. & C.T. Robinson. 1868. Descriptions of American Lepidoptera. – No. 3. Transaction of the American Entomological Society. 323–360.

Hebert, P.D.N., A. Cywinska, S.L. Balland, & J.R. deWaard. 2003. Biological identifications through DNA barcodes. Proc. Royal Soc. B 270:313–321.

Hodges, R.W. 1971. Sphingoidea. The moths of America north of Mexico including Greenland. Fascicle 21. E. W. Classey, London.

Hundsdoerfer, A.K., I.J. Kitching, & M. Wink. 2005. A molecular phylogeny of the hawkmoth genus Hyles (Lepidoptera: Sphingi-

dae, Macroglossinae). Mol. Phylogenet. Evol. 35:442–458.
JONES, J.R.J.L. 1951. An annotated check list of the Macrolepidoptera of British Columbia. Occasional paper no. 1. The Entomological Society of British Columbia. 148 pp.
KITCHING, I.J. & J.-M. CADIOU. 2000. Hawkmoths of the world: An annotated and illustrated revisionary checklist. Cornell University Press, Ithaca, and The Natural History Museum, London. 226 pp.
LAFONTAINE, J.D. 2004. Noctuoidea: Noctuidae (part), Noctuinae (part - Agrotini). In: R.W. Hodges (ed.). The moths of North America, fasc. 27.1. Washington, DC: Wedge Entomological Research Foundation.
NATURAL RESOURCES CANADA. 2006. Canadian Geographical Names Data Base. http://geonames.nrcan.gc.ca/search/search_e.php.
RIOS, N.E., & H.L. BART. 2004. GEOLocate Georeferencing Software. Tulane, LA: Tulane Museum of Natural History. http://www.museum.tulane.edu/geolocate/default.aspx
ROTHSCHILD, L.W.R. & K. JORDAN. 1903. A revision of the lepidopterous family Sphingidae. Novitates Zool. 9 Suppl.
SMYTH, E.A. 1900. Identity of *Hemaris tenuis* and *Hemaris diffinis*. Entomol. News 11:584–589.
STRECKER, F.H.H. 1878. In: Ruffner, Ann. Rep. Chief of Engineers, App. SS for 1878: 1858, pl. 2, fig. 1.
SWOFFORD, D.L. 2002. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4.0b10. Sunderland, Massachusetts: Sinauer Associates.
TUTTLE, J.P. 2007. The hawk moths of North America. The Wedge Entomological Research Foundation. Washington, DC. 253 pp.

Received for publication on 27 March 2008; revised and accepted on 16 October 2008.

Journal of the Lepidopterists' Society
63(2), 2009,110-117

SEED CAPSULE PRODUCTION IN THE ENDANGERED WESTERN PRAIRIE FRINGED ORCHID (*PLATANTHERA PRAECLARA*) IN RELATION TO SPHINX MOTH (LEPIDOPTERA: SPHINGIDAE) ACTIVITY

CHRISTIE BORKOWSKY
Critical Wildlife Habitat Program, Manitoba Conservation, Box 24, 200 Saulteaux Cres., Winnipeg, Manitoba, Canada R3J 3W3

AND

A. RICHARD WESTWOOD
University of Winnipeg, Department of Biology, 515 Portage Ave., Winnipeg, Manitoba, Canada R3B 2E9; email: r.westwood@uwinnipeg.ca

ABSTRACT. The endangered western prairie fringed orchid, *Platanthera praeclara* Sheviak and Bowles, is found in remnant tall grass prairie in the northern central plains of North America. The Canadian population of the western prairie fringed orchid produces fewer seed capsules compared to more southern populations in the United States. Pollen vectors of the western prairie fringed orchid include two species of sphinx moths (Sphingidae) in Canada and the orchid can be considered a pollen limited species. The degree to which the presence of sphinx moths may affect pollination success in the western prairie fringed orchid was evaluated using ultraviolet lights to attract sphinx moths and increase nectar feeding activity, thus potentially increasing seed capsule production. Ultraviolet lights were tested at two levels of illuminance. Significantly more individual flowers and plants developed seed capsules in plots with ultraviolet lights than in plots without lights. The number of flowers per plant was unrelated to the number of seed capsules produced per plant. It appears sphinx moth pollinators were equally attracted to small, medium and large sized orchid inflorescences. The degree to which high winds may also decrease the pollinating activity of sphinx moths within the vicinity of orchids is considered. Results indicate that ultraviolet lights may be useful to temporarily manipulate seed capsule production.

Additional key words: western prairie fringed orchid, *Platanthera praeclara*, seed capsules, pollination, sphinx moths, *Sphinx drupiferarum*, *Hyles gallii*.

The endangered western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles) is found in wet sedge meadows in remnant tall grass prairie located in the central plains of North America (Smith 1993; Wolken *et al.* 2001). Loss of habitat is considered the primary cause of its endangered status in Canada and the United States (Davis 1994; U.S. Fish and Wildlife Service 1996), with tall grass prairie being considered one of the most endangered ecosystems in North America (Joyce & Morgan 1989; Samson & Knopf 1994; Hamilton 2005; Whiles & Charlton 2006). When in bloom, these orchids grow 38–85 cm tall and can produce 20 or more flowers, which are arranged on a single racemose spike that opens from the bottom to the top of the inflorescence (Sheviak & Bowles 1986; Pleasants 1993; Pleasants & Moe 1993). The creamy white flowers emit a sweet fragrance that becomes more intense in the late evening during the blooming period of mid June to early July (Sheviak & Bowles 1986). The most striking visual characteristics of the flowers are the large, deeply fringed tri-lobed lower lip and long, slender nectar spur. The only known pollen vectors of *P. praeclara* are several species of sphinx moths (Sphingidae) (Sheviak & Bowles 1986; Cuthrell 1994; Westwood & Borkowsky 2004). Westwood & Borkowsky (2004) described pollination of the Canadian population of the western prairie fringed orchid by two sphinx moths: the wild cherry sphinx, *Sphinx drupiferarum* J.E. Smith and the bedstraw hawkmoth, *Hyles gallii* (Rottenburg) by trapping moths in the act of pollinating individual plants.

The pollen of the orchid is packaged in two pollinaria located on each side of the stigma. Each pollinarium is composed of three structures: the pollinia (pollen masses), the caudicle and a sticky disk called the viscidium (Pleasants & Moe 1993; Johnson & Edwards 2000; Pacini & Hesse 2002). The mechanism of pollen removal from the flower by nectar-seeking sphinx moths involves the adherence of the viscidium to the eye of the sphinx moth. The entire pollinarium is removed from the flower when the moth withdraws its proboscis and moves to another flower where the pollinia may contact the stigma and fertilize the flower (Sheviak & Bowles 1986; Westwood & Borkowsky 2004).

The number of female flowers produced by an individual plant reflects the maximum number of fruits that the plant can produce (Stephenson 1981), but individuals of many plant species produce more flowers than mature fruits (Ågren *et al.* 2008; Spigler & Chang 2008). Flowers and immature fruits may be damaged by environmental phenomena (Inouye 2000; Pilson 2000) or predators (Ågren *et al.* 2008), such that flowers

cannot be pollinated or the fruit cannot fully mature. Undamaged flowers often fail to initiate fruit (Stephenson 1981; Heithaus *et al.* 1982) and this disparity between flower and fruit production (as exhibited by the western prairie fringed orchid, which is a self-compatible, facultative out-crosser) is usually attributed to factors that limit fruit production by inhibiting pollination, often by reduced pollinator visitation rates (Roll *et al.* 1997; Parra-Tabla *et al.* 1998; Mattila & Kuitunen 2000; Rathcke 2000; Spigler & Chang 2008). Such plants are said to be pollen limited.

Westwood & Borkowsky (2004) noted a substantially lower level of annual seed capsule production in the Canadian population compared with more southern populations. While the regulation of the level of seed capsule production in the western prairie fringed orchid may be linked to several factors including site quality and herbivory, the abundance of sphinx moth pollinators may also be a factor.

Local abundance of Sphingidae may vary greatly between years (Hodges 1971; Duarte & Schlinwein 2005; Tuttle 2007). Adult sphinx moth surveys indicated that low levels of seed capsule development in the Canadian population of the orchid may be related to a scarcity of pollinators or perhaps environmental factors that diminish pollinator effectiveness (Westwood & Borkowsky 2004). *Sphinx drupiferarum* is uncommon in Manitoba and populations of *Hyles gallii* fluctuate widely on an annual basis with adults being almost absent in some years (Westwood & Borkowsky 2004). Other species of sphinx moths have been identified as pollinators of the orchid in the southern parts of the range (Sheviak & Bowles 1986; Cuthrell 1994; Ralston *et al.* 2008), although most do not occur in Canada. The area surrounding western prairie fringed orchid habitat in Manitoba has become fragmented by agricultural land use ranging from tame pasture to cropland, with insecticide and herbicide usage, and there may be limited habitat available for sphinx moth pollinators. Alternately, environmental factors such as high wind speeds may limit pollinator-orchid contact during the bloom period (Eisikowitch & Galil 1971; Willmott & Búrquez 1996).

We hypothesized that the western prairie fringed orchid population in Canada is pollen limited and that increased visits by sphinx moths would increase seed capsule production. In order to examine the degree to which sphinx moth nectar seeking activity may affect rates of seed capsule production we designed an experiment to artificially attract sphinx moth pollinators to orchid habitat. We hypothesized that ultraviolet lights would attract and hold sphinx moths in the vicinity of orchids compared to areas of orchids without lights, and through increased moth feeding activity there would be a measurable increase in seed capsule production. This increased level of seed capsule production would be an indirect measure of sphinx moth feeding activity. We also examined the effect of individual plant inflorescence size on the number of seed capsules produced, postulating that taller plants with more flowers would be more accessible and attractive to nectar seeking moths. Finally we report on nightly wind speeds in orchid plots and the potential influence on sphinx moth activity.

Study Area and Methods

Study area. The Manitoba Tall Grass Prairie Preserve (hereafter called the Preserve) is located in southeastern Manitoba near the Canada-United States border (49° 05' N, 96° 49' W). The Preserve represents the only known location in Canada where the western prairie fringed orchid occurs (Borkowsky & Jones 1998). The nearest population is located in northwest Minnesota approximately 125 km to the south of the Preserve.

The climate is continental, with an average of 579.1 mm of precipitation annually, a mean summer temperature of 19.6 °C and a mean winter temperature of -18.8 °C (Moore & Fortney 1994). The soil is grey-wooded podzol, having a sandy-loam to clay-loam texture with frequent rock outcrops. The shallow slope of the landscape (1–3%), poor drainage and high water table (within 3m of the surface) generally inhibits agricultural productivity within the Preserve.

The natural vegetation in the Preserve and surrounding area may be grouped into three general communities: aspen woodland, upland prairie and sedge meadow. The areas recognized as aspen woodland are dominated by aspen (*Populus tremuloides* Michx.), interspersed with bur oak (*Quercus macrocarpa* Michx.) and shrubs including saskatoon (*Amelanchier alnifolia* Nutt.), chokecherry (*Prunus virginiana* L.) and hazelnut (*Corylus* spp.). The herbaceous layer is dominated by poison-ivy (*Rhus radicans* L.), meadow rue (*Thalictrum* spp.), goldenrod (*Solidago* spp.), golden alexander (*Zizia aurea* (L.) Koch) and various graminoids. The upland prairie is dominated by big blue stem (*Andropogon gerardi* Vitman) and Indian grass (*Sorghastrum nutans* (L.) Nash) and forbs such as purple prairie clover (*Petalostemum purpureum* (Vent.) Rydb.), wild strawberry (*Fragaria virginiana* Dcne.), goldenrod (*Solidago* spp.) and sunflower (*Helianthus* spp.). Shrubs such as shrubby cinquefoil (*Potentilla fruticosa* L.) and rose (*Rosa* spp.) occur in the upland prairie. The sedge meadow where the orchids are most common is dominated by various sedges (*Carex* spp.)

and rushes (*Juncus* spp.) along with prairie cord grass (*Spartina pectinata* Link), swamp birch (*Betula glandulosa* Michx.) and several species of willows (*Salix* spp.) (Looman & Best 1987; Moore & Fortney 1994).

Field sites. Prior to experimental plot selection, inventory assessments of western prairie fringed orchids from previous growing seasons and general orchid distribution maps for the Preserve were examined to establish potential plot locations (Davis 1994; Borkowsky & Jones 1998). Orchids tend to grow in aggregations and flowering stems become visible in late May (*i.e.*, height of stems approximately 10 cm). The number of flowering stems varies greatly from year to year in the Preserve. In 2001, six plots were selected, each with a minimum of 30 orchid plants that would produce a flowering stem. Plots were separated by a minimum of 500m and were surrounded to some degree by aspen woodland such that they were not visible at 3m above the ground from adjacent plots. Plots were randomly assigned one of two treatments: ultraviolet light or no ultraviolet light (left in a natural state). The three plots assigned to the ultraviolet light treatment were labelled UV-P1, UV-P2, and UV-P3 and the plots without lights NAT-P1, NAT-P2, and NAT-P3. Eight plots (four with ultraviolet lights and four left in a natural state) were used in 2002 as more flowering stems were present.

Sampling methods. In June 2001, the center of each plot was marked with an orange pin flag, and a 60m radius, covering approximately 1.13 ha, was marked with eight additional pin flags to delineate the circumference of the plot. An ultraviolet light covered by a small wooden panel (1m × 1m) was placed in the center of ultraviolet light plots approximately one meter above the ground. The ultraviolet light and its power source were located underneath the panel to prevent water damage to the electrical components. The ultraviolet light used in this study consisted of a single 8 watt florescent bulb assembly from a Ward's® All Weather Insect Bucket Trap which was powered by a 12 volt marine deep cycle battery. A translucent white cloth cover was placed over each light in 2001. In the first year of the study the cover was used to lower the intensity of light emission so as to minimize the visibility of lights from plots without lights. The intensity of the light measured at 0.3m from the cloth covered light was approximately 5.5 ft. candles. The cloth cover was not used in 2002 to test the lights at their maximum intensity (approximately 10.2 ft. candles at 0.3m). In both years, the ultraviolet light was operated on alternate nights between 2000 and 0800 h throughout the flowering period. The ultraviolet lights were operated for 13 nights beginning on 25 June 2001 and nine nights beginning on 6 July 2002. Lights were not placed in natural plots to ensure they resembled normal orchid habitat and sphinx moths did not use them as protective diurnal resting places, which may increase their night nectar foraging activity around orchids. Lights in ultraviolet light plots were examined each morning for the presence of resting sphinx moths.

To estimate the effect of wind on sphinx moth activity the wind speed (km/hr) was recorded during the bloom period on an hourly basis over a 24 hr period (Environment Canada 2008) for each day to determine a mean daily wind speed and also to calculate the mean wind speed for the time period of 2000–0500 h (the period when sphinx moth pollinators are active in the Preserve).

Data analysis. The number of flowers (*i.e.*, inflorescence size), pollinaria available, pollinaria removed, and seed capsules produced were recorded for each plant in 2001 and 2002. Pollinaria removal and seed capsule production have been widely used as proxy measures to gauge sphinx moth feeding activity as direct observation of sphinx moths is difficult due to their nocturnal habit and swift flight (Sheviak & Bowles 1986; Pleasants & Moe 1993; Cuthrell 1994). We calculated the mean number of flowers per plant, and number and percent of pollinaria removed. Number of seed capsules per plant and per flower was calculated for each plot to standardize per capita capsule and flower production. All experimental variables were tested for departure from the normal distribution and transformed where necessary (Zar 1996). Untransformed means are reported in the Results and Tables.

Visual inspection of flowering plant heights and number of flowers per orchid in previous field investigations revealed that plants generally grouped into three broad categories. Smaller plants were well below surrounding vegetation, medium sized plants were approximately level with surrounding sedges, rushes and grasses and larger orchids were often 10 or more cm above the surrounding vegetation. A histogram examination of plant height and number of flowers per plant in 2001 and 2002 confirmed the three broad categories. We postulated that sphinx moths may prefer tall plants with many flowers to maximize ease of nectar collection versus visiting short plants with few flowers partially covered by other herbs and grasses. Three plant size categories were established including small sized plants (1 to 3 flowers), medium sized plants (4 to 10 flowers) and large sized plants (11 or more flowers). The mean number of flowers per plant and standard deviation (7.1 ± 2.8) of all plants was calculated from the pooled 2001 and 2002 data set. The mean and standard deviation were considered to be the medium size

category (*i.e.* 4 to 10 flowers per plant).

Plots were used as replicates (and assumed to be independent) for plot type comparisons. Each variable (flowers per plant, percent pollinaria removed, seed capsules per plant and per flower, inflorescence size category) was tested for differences between plot type and the interaction of plot type and inflorescence size using a general linear model (α = 0.05). Fisher's least significant difference (LSD) post hoc test was used to separate means when ANOVA was significant for tests between plant inflorescence size categories. An independent t test was used to compare the number of plants in plots by inflorescence size and wind speeds between bloom periods in 2001 and 2002. All statistical analyses were done using SPSS v. 11.0.1 (SPSS Inc. 2001).

RESULTS

The mean number of flowers per plant was 7.1 ± 0.2 and 7.3 ± 0.1 for plots in 2001 and 2002, respectively (Table 1). In 2001 mean percent pollinaria removal was not significantly different between plots with ultraviolet lights (12.9 ± 2.3) and those without lights (10.1 ± 3.6) ($F_{1,4}$ = 0.42, p = 0.550). In 2002 mean percent pollinaria removal was significantly different between the ultraviolet light plots (7.8 ± 0.5) and plots without lights (6.2 ± 0.2) ($F_{1,6}$ = 8.94, p = 0.024).

Total seed capsule production in 2001 and 2002 was 11 and 226 capsules, respectively (Table 1). Mean number of seed capsules per plant was not significantly different between the ultraviolet light plots and plots without lights in 2001 ($F_{1,4}$ = 0.01, p = 0.936) (Table 1). In 2002 number of seed capsules per plant was significantly different between treatments, 0.35 ± 0.02 for the ultraviolet light plots and 0.21 ± 0.02 for plots without lights ($F_{1,6}$ = 21.46, p = 0.004) (Table 1).

In 2001, mean number of seed capsules per flower (Table 1) was not significantly different between the ultraviolet light plots and plots without lights ($F_{1,4}$ = 0.76, p = 0.431). In 2002 the difference in seed capsule production per flower was significant ($F_{1,6}$ = 19.43, p = 0.005), with the number of seed capsules per flower in the ultraviolet light plots almost twice that of plots without lights (0.051 ± 0.004 and 0.028 ± 0.003, respectively) (Table 1).

When plants were placed in inflorescence size categories in 2001, 37.8%, 40.8% and 21.4% of plants fell into the small, medium and large size groups, respectively (Table 2). There was no significant difference in the number plants in the medium and large inflorescence size categories between the plots with ultraviolet lights and without (t_4 = -0.91, p = 0.412; t_4 = -1.05, p = 0.350 respectively). There were significantly more small plants in the ultraviolet light plots than plots without lights in 2001 (t_4 = -4.17, p = 0.014).

In 2002, 29.4%, 49.9% and 20.7% of plants were assigned to the small, medium and large inflorescence groups, respectively (Table 2). There was no significant difference in the number plants in all inflorescence size categories between the plots with ultraviolet lights and without in 2002 (small - t_6 = -0.78, p = 0.465; medium - t_6 = -1.13, p = 0.299; large - t_6 = -1.17, p = 0.285; respectively). The percentage of large inflorescence plants in all plots was similar in 2001 and 2002, although the percentage of smaller plants decreased in 2002 while the number of medium sized plants increased. There was no significant difference in the number of capsules per plant or per flower between plots with ultraviolet lights and those without for all three inflorescence size comparisons in 2001 (Table 3). In 2002, medium sized inflorescences produced more capsules per plant and per flower in ultraviolet light plots than plots without lights (Table 2). When number of seed capsules produced by inflorescence size was pooled over all plots there was a noticeable trend of increasing number of seed capsules with inflorescence size, although the trend was only significant for number of capsules per plant in 2002. There was no significant interaction between the number of seed capsules produced per plant or per flower by inflorescence size and plot type in 2001 ($F_{5,12}$ = 0.03, p = 0.969; $F_{5,12}$ = 0.14, p = 0.872, respectively) or 2002 ($F_{5,18}$ = 0.82, p = 0.455; $F_{5,18}$ = 1.13, p = 0.350) (Table 3).

The mean daily wind speed over the bloom period was 12.7 ± 1.2 and 12.2 ± 1.1 km/hr in 2001 and 2002, respectively. The mean wind speed over the bloom period from 2000-0500 h was 9.5 ± 0.9 and 9.8 ± 1.1 km/hr in 2001 and 2002, respectively. There was no significant difference in mean daily wind speeds between 2001 and 2002 during the bloom period or the approximate 9 hour period when sphinx moth pollinators are most active (24 hrs: t_{40} = 0.31, p = 0.756; 9 hr period: t_{40} = -0.25, p = 0.800).

There was no evidence that adult sphinx moths used the ultraviolet lights for shelter during the day in either year of the study.

DISCUSSION AND CONCLUSION

The mean number of flowers per plant in the present study ranged from 5.4 to 8.5. These values are consistent with the range of 7.0 to 9.4 flowers per plant documented by Pleasants (1993) in Minnesota and North Dakota. However, these values were less than an average of 12.6 flowers per plant reported by Sheviak &

Table 1. Plot summaries for plant, flower and seed capsule variables of flowering western prairie fringed orchids sampled in 2001 and 2002.

Year	Plot[1]	Number of plants	Number of flowers	Number of seed capsules	Seed capsules per plant	Seed capsules per flower	Inflorescence Size[2] Mean ± SE	Inflorescence Size[2] Range	No. Pollinaria Available	No. Pollinaria Removed	% Pollinaria removed
2001	UV-P1	51	320	0	0.000	0.000	6.3 ± 0.5	1 - 16	640	108	16.9
	UV-P2	65	352	6	0.092	0.017	5.4 ± 0.3	2 - 12	704	94	13.3
	UV-P3	68	503	0	0.000	0.000	6.4 ± 0.3	3 - 12	1006	88	8.7
	NAT-P1	99	855	2	0.020	0.002	8.5 ± 0.4	3 - 16	1710	84	4.9
	NAT-P2	75	560	1	0.013	0.001	7.5 ± 0.4	2 - 18	1120	191	17.0
	NAT-P3	29	181	2	0.068	0.110	6.6 ± 0.5	2 - 13	362	31	8.6
Total/Mean		387	2771	11	0.032	0.022	6.9 ± 0.2		5542	596	11.6
2002	UV-P1	87	532	28	0.322	0.053	6.1 ± 0.2	1 - 13	1064	71	6.7
	UV-P2	91	706	32	0.352	0.045	7.8 ± 0.3	1 - 16	1412	123	8.7
	UV-P3	151	1121	50	0.331	0.045	7.4 ± 0.2	1 - 18	2242	160	7.1
	UV-P4	25	159	10	0.400	0.063	6.4 ± 0.4	2 - 11	318	27	8.5
	NAT-P1	150	1068	35	0.233	0.033	7.1 ± 0.2	2 - 20	2136	132	6.2
	NAT-P2	150	1200	33	0.220	0.028	8.0 ± 0.2	2 - 17	2400	141	5.9
	NAT-P3	91	631	12	0.132	0.019	6.9 ± 0.3	1 - 6	1262	75	5.9
	NAT-P4	106	810	26	0.245	0.032	7.6 ± 0.2	3 - 15	1620	111	6.8
Total/Mean		851	6227	226	0.279	0.040	7.3 ± 0.1		12454	840	7.0

[1] UV = Ultraviolet light plot; NAT = Natural plot.

[2] Mean number of flowers per plant.

Table 2. Number of plants per plot based on plant inflorescence size in 2001 and 2002.

2001 Inflorescence size	2001 Plot[1]	2001 Number of plants	2001 Total Plants per plot type/ mean ± SE	2002 Inflorescence size	2002 Plot[1]	2002 Number of plants	2002 Total Plants per plot type/ mean ± SE
Small	UV-P1	29		Small	UV-P1	39	
< 4 flowers	UV-P2	36		< 4 flowers	UV-P2	22	
	UV-P3	29	94/31.3±2.3		UV-P3	38	
	NAT-P1	16			UV-P4	10	109/27.2±6.9
	NAT-P2	22			NAT-P1	56	
	NAT-P3	14	52/17.3±2.4		NAT-P2	31	
					NAT-P3	28	
					NAT-P4	25	140/35.0±7.0
Medium	UV-P1	13		Medium	UV-P1	37	
4-10 flowers	UV-P2	23		4-10 flowers	UV-P2	48	
	UV-P3	27	63/21.0±4.1		UV-P3	80	
	NAT-P1	48			UV-P4	13	178/44.5±13.9
	NAT-P2	36			NAT-P1	63	
	NAT-P3	11	95/31.6±10.9		NAT-P2	74	
					NAT-P3	51	
					NAT-P4	57	245/61.2±4.9
Large	UV-P1	9		Large	UV-P1	11	
> 10 flowers	UV-P2	6		> 10 flowers	UV-P2	21	
	UV-P3	12	27/9.0±1.7		UV-P3	33	
	NAT-P1	35			UV-P4	2	67/16.7±6.6
	NAT-P2	17			NAT-P1	31	
	NAT-P3	4	56/18.6±8.9		NAT-P2	45	
					NAT-P3	12	
					NAT-P4	24	109/28.0±6.9

[1] UV = Ultraviolet light plot; NAT = Natural plot.

Table 3. Effect of inflorescence size on seed capsule production in the western prairie fringed orchid in 2001 and 2002.

2001				2002			
Inflorescence size	Plot[1]	Seed capsules per plant	See capsules per flower	Inflorescence size	Plot	Seed capsules per plant	Seed capsules per flower
Small	UV n = 3	0.018 ± 0.008	0.005 ± 0.001	Small	UV n = 4	0.162 ± 0.082	0.037 ± 0.018
< 4 flowers	NAT n = 3	0.000 ± 0.00	0.000 ± 0.00	< 4 flowers	NAT n = 4	0.013 ± 0.005	0.000 ± 0.000
	$F_{1,4}$ P	1.01, 0.373	1.00, 0.375		$F_{1,6}$ P	1.55, 0.260	1.60, 0.252
Medium	UV n = 3	0.029 ± 0.013	0.004 ± 0.004	Medium	UV n = 4	0.403 ± 0.054	0.056 ± 0.008
4-10 flowers	NAT n = 3	0.037 ± 0.027	0.005 ± 0.003	4-10 flowers	NAT n = 4	0.130 ± 0.003	0.017 ± 0.001
	$F_{1,4}$ P	0.43, 0.845	0.014, 0.912		$F_{1,6}$ P	24.62, 0.003	21.56, 0.004
Large	UV n = 3	0.111 ± 0.011	0.010 ± 0.009	Large	UV n = 4	0.506 ± 0.172	0.044 ± 0.015
> 10 flowers	NAT n = 3	0.112 ± 0.069	0.113 ± 0.007	> 10 flowers	NAT n = 4	0.453 ± 0.088	0.039 ± 0.007
	$F_{1,4}$ P	0.001, 0.990	0.003, 0.962		$F_{1,6}$ P	0.07, 0.794	0.112, 0.749
Infloresecense	Small n = 6	0.009 ± 0.009	0.002 ± 0.002	Infloresecense	Small n = 8	0.109 ± 0.044a[2]	0.025 ± 0.010
Size	Medium (n = 6)	0.033 ± 0.017	0.004 ± 0.002	Size	Medium (n = 8)	0.267 ± 0.057b	0.036 ± 0.008
	Large (n = 6)	0.111 ± 0.058	0.011 ± 0.005		Large (n = 8)	0.479 ± 0.090c	0.042 ± 0.008
	$F_{2,15}$ P	2.25, 0.140	1.22, 0.322		$F_{2,15}$ P	7.72, 0.003	0.931, 0.410

[1] UV = Ultraviolet light plot; NAT = Natural plot.

[2] Means in columns followed by different letters are significantly different (Fishers LSD, $p < 0.05$)

Bowles (1986), who examined orchids from locations across the range of *P. praeclara* in the United States, including states at the southern extent of the orchid's range (Iowa, Nebraska and Kansas). The longer and warmer growing season in the southern part of the orchid's range may produce on average larger plants with more flowers.

To be an effective pollinating agent, a sphinx moth must remove at least one of the pollinaria from an orchid flower and then subsequently visit an unpollinated flower. Increased feeding activity by sphinx moths should presumably lead to an increased number of pollinaria removed. In 2001, the difference in the percent pollinaria removed between the two plot types was not significant, while in 2002 a significantly higher percentage of pollinaria were removed in ultraviolet light plots versus plots without lights, which corresponded to a difference in seed capsule production between plot types. In 2001 and 2002, levels of pollinaria removal in our study in both plot types were considerably lower than levels recorded under natural conditions in North Dakota (33%) (Pleasants & Moe 1993). Sphinx moth pollinator populations may be lower in our study area.

In the present study the overall mean percent pollinaria removed was higher in 2001 (11.6%) than 2002 (7.0%). Pleasants (1993) found a similar difference between study years with overall site averages of 33% and 8% for 1991 and 1992, respectively. Sphinx moth populations may fluctuate from year to year, and between year differences in pollinaria removal may be a result of their fluctuating local abundance (Westwood & Borkowsky 2004). Although the rate of pollinaria removal in 2001 in all plots combined was higher than in 2002, the number of seed capsules produced per plant and per flower in 2002 was more than double that recorded in 2001. While pollinaria removal and subsequent seed capsule production were significantly higher in ultraviolet light plots versus plots without lights in 2002, using only pollinaria removal as an indicator of overall sphinx moth activity needs to be further investigated. During the current study it was incidentally observed that occasionally orchid pollinaria were attached to the ends of orchid petals (although never on the orchid stigmatic surface) and other surrounding vegetation, particularly the leaves of tall grasses such as big blue stem and Indian grass. Cuthrell (1994) suggested that wind may cause accidental pollinaria removal. During windy periods, the inflorescence may contact stems and leaves of surrounding vegetation, especially grasses that equal or exceed the height of the orchid. The combined action of vegetation becoming entangled with the orchid flowers and wind movement could cause pollinaria to adhere to adjacent vegetation (Cuthrell 1994). Thus seed capsule production should be used as the best indicator of pollination success.

In our study wind speeds over the bloom period were very similar in 2001 and 2002. If wind was a major factor in causing a higher percent of pollinaria to be removed

in 2001 it is not reflected by wind speed measurement. It is also unlikely that sphinx moths were responsible for the higher pollinaria removal rate in 2001 as there was not a corresponding higher percentage of seed capsules produced. Although seed capsule production is the most accurate measure of sphinx moth activity, orchids have to be carefully monitored as pods take several months to fully develop and orchids may be susceptible to herbivory by a variety of mammals.

Wind can also affect a pollinator's ability to travel between plants. Eisikowitch & Galil (1971) observed a correlation between wind speed and levels of pollination and seed production in an Israeli amaryllis, *Pancratium maritimum* L. Sphinx moth flower visits were common when wind speeds were below 2 m/s, resulting in the highest levels of pollination and seed set (Eisikowitch & Galil 1971). Pollination did not occur when wind speeds were greater than 3 m/s as the sphinx moths did not travel between flowers; wind speeds between 2 and 3 m/s reduced the flight activities of the sphinx moth pollinators and resulted in lower levels of pollination and seed set (Eisikowitch & Galil 1971). Sphinx moth visitations to the flowers of *Merremia palmeri* (S. Wats.) Hallier ended when winds were gusty or became moderately strong (Willmott & Búrquez 1996). We found wind speeds ranged from approximately 2.6 to 2.7 m/s (9.5 to 9.8 km/hr) during the nocturnal pollination period for sphinx moths. These wind speeds are probably close to the upper limit for sphinx moth pollinating activity in the Preserve. High winds during the short bloom period of *P. praeclara* may be a significant factor in reducing seed capsule production and may help explain the large variation in the annual level of seed capsule production. In the Preserve, orchids grow in exposed open areas of prairie and sphinx moths may prefer sheltered areas to seek nectar on windy nights. Future research should examine the effects of wind on both sphinx moth activity and the loss of pollinaria to surrounding vegetation.

In 2002, the increased seed capsule production in the plots with ultraviolet lights may have been due, in part, to removal of the cover sheet to maximize the attractiveness of the plots, although we could not test this effect directly by actually observing moths. The collecting distance of light traps is estimated to be less than 10m (Frank 1988; Southwood & Henderson, 2000) thus there was little chance that moths in one plot could have been attracted by a light from another plot. We hypothesize that moths were probably not attracted from a significant distance (greater than 10m) to plots with ultraviolet lights, but that once attracted by the odor of the orchids and/or visual cues they may have remained in the vicinity of the light and continued to nectar feed in the plot. It appears that the maximum intensity of the light was required to attract moths. It is known that sphinx moths attracted to lights may remain quiescent in the vicinity of lights until daylight (Hodges 1971; Pittaway 1993; Duarte & Schlinwein 2005; Tuttle 2007), and as lights were activated once every 48 hours in our study it is reasonable to expect that moths attracted to the ultraviolet lights may have remained in the plot or the immediate vicinity up to several days.

Less than 7% of flowers produced seed capsules in our study. Seed capsule production rates four to six times greater have been recorded for *P. praeclara* in Minnesota and North Dakota (Pleasants 1993; Pleasants & Moe 1993). Seed capsule production rates in the current study were well below the 49.3% average (range 13.6 to 79.0%) for 11 other North American nectariferous orchids (Neiland & Wilcock 1998).

In 2002 orchids in the medium sized inflorescence category (4–10 flowers) had more seed capsules per plant in the plots with ultraviolet lights than plots without lights. There was also a trend for more seed capsules per plant and per flower to be produced as the size of the inflorescence increased in both years when all plots were pooled, but it was not significant. We could not demonstrate that sphinx moth pollinators had a consistent preference for small, medium or large sized inflorescences. Under natural pollination conditions, Pleasants & Moe (1993) found that seed capsule production was not correlated to the number of flowers in the inflorescence; however, they did not use size categories as we did in the current study.

There are few reported studies that test ultraviolet light as a means of attracting beneficial insects such as pollinators (Nabli *et al.* 1999). Regulations governing the endangered status of the orchid in Manitoba prevent any direct manipulation of large numbers of plants, including removal of flower parts to investigate pollination rates and seed capsule production through the use of techniques such as hand pollination. As the removal of seed capsules from western prairie fringed orchids is not permitted, the temporary use of ultraviolet lights in patches of orchids may attract sphinx moths and inherently increase levels of seed capsule production above natural levels so that capsules can be removed for other research purposes. Successful seed capsule formation in *P. praeclara* is entirely dependent on sphinx moth nectar feeding activity, and in our study, application of ultraviolet lights in prairie habitat significantly increased seed capsule production in *P. praeclara*.

ACKNOWLEDGEMENTS

The authors thank K. Budnick, J. Greenall, C. Hamel, P. West-

horpe, R. Currie, B. Ford, L. Heshka and L. Reeves for assistance with this project. C. Friesen provided advice and assisted with manuscript preparation. This study was funded by the Manitoba Orchid Society, World Wildlife Fund, Manitoba Sustainable Development Fund, Manitoba Conservation and the University of Winnipeg.

LITERATURE CITED

ÅGREN, J., J. EHRLEN, & C. SOLBRECK. 2008. Spatio-temporal variation in fruit production and seed predation in a perennial herb influenced by habitat quality and population size. J. Ecology 96: 334–345.

BORKOWSKY, C.L. & R.E. JONES. 1998. Manitoba Tall Grass Prairie Preserve—natural resources inventory V. Project Report No. 99–03W. Manitoba Department of Natural Resources.

CUTHRELL, D.L. 1994. Insects associated with the prairie fringed orchids, *Platanthera praeclara* Sheviak & Bowles and *P.* leucophaea (Nuttall) Lindley. MSc. Thesis. North Dakota State University. Department of Entomology.

DAVIS, S.K. 1994. Manitoba Tall Grass Prairie Preserve—natural resources inventory I. Manitoba Department of Natural Resources. Project Report No. 98-03W.

DUARTE, J.A., JR. & C. SCHLINDWEIN. 2005. The highly seasonal hawkmoth fauna (Lepidoptera: Sphingidae) of the Caatinga of northeast Brazil: a case study in the state of Rio Grande do Norte. J. Lepid. Soc. 59: 212–218.

ENVIRONMENT CANADA. 2008. Canadian daily climate data. Meteorological Service of Canada.

EISIKOWITCH, D. & J. GALIL. 1971. Effect of wind on the pollination of *Pancratium maritimum* L. (Amaryllidaceae) by hawkmoths (Lepidoptera: Sphingidae). J. Animal Ecology 40: 673–678.

FRANK, K.D. 1988. Impact of outdoor lighting on moths: an assessment. J. Lepid. Soc. 42: 63–93.

HAMILTON, K.G.A. 2005. Bugs reveal an extensive, long-lost northern tallgrass prairie. BioScience 55: 49–59.

HEITHAUS, E.R., E. STASHKO, & P.K. ANDERSON. 1982. Cumulative effects of plant-animal interactions on seed predation by *Bauhinia ungulata*, a neotropical legume. Ecology 63: 1294–1302.

HODGES, R.W. 1971. The moths of America north of Mexico. Fascicle 21. Sphingoidea. E.W. Classey Ltd. & R.B.D. Publications Inc. London.

INOUYE, D.W. 2000. The ecological and evolutionary significance of frost in the context of climate change. Ecology Letters 3: 457–463.

JOHNSON, S.D. & T.J. EDWARDS. 2000. The structure and function of orchid pollinaria. Plant Systematics and Evolution 222: 243–269.

JOYCE, J. & J.P. MORGAN. 1989. Manitoba's tall grass prairie conservation project. Pp. 71–74 *In* T.B. Bragg and J. Stubbendiuk (eds.), Proceedings of the eleventh North American Prairie Conference. University of Nebraska, Lincoln, Nebraska.

LOOMAN, J. & K.F. BEST. 1987. Budd's flora of the Canadian prairie provinces. Publication 1662. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada.

MATTILA, E. & M.T. KUITUNEN. 2000. Nutrient versus pollination limitation in *Platanthera bifolia* and *Dactylorhiza incarnate* (Orchidaceae). Oikos 89: 360–366.

MOORE, J.R. & G. FORTNEY (eds.). 1994. Management plan for the tall-grass prairie preserve in Manitoba. Critical Wildlife Habitat Program. Winnipeg, Manitoba.

NABLI, H., W.C. BAILEY, & S. NECIBI. 1999. Beneficial insect attraction to light traps with different wavelengths. Biological Control 16: 185–188.

NEILAND, M.R.M. & C.C. WILCOCK. 1998. Fruit set, nectar reward, and rarity in the Orchidaceae. American J. Botany 85: 1657–1671.

PACINI, E. & M. HESSE. 2002. Types of pollen dispersal units in orchids, and their consequences for germination and fertilization. Annals Botany 89: 653–664.

PARRA-TABLA, V., C.F. VARGAS, & L.E. EGUIARTE. 1998. Is *Echeveria gibbiflora* (Crassulaceae) fecundity limited by pollen availability? An experimental study. Functional Ecology 12: 591–595.

PILSON, D. 2000. Herbivory and natural selection on flowering phenology in wild sunflower, *Helianthus annuus*. Oecologia 122: 72–82.

PITTAWAY, A.R. 1993. Hawkmoths of the western Palaearctic. Pittaway, Harley Books, Colchester.

PLEASANTS, J.M. 1993. Pollination ecology of the western prairie fringed orchid, *Platanthera praeclara*. Parks and Tourism Department, North Dakota.

_____ & S. MOE. 1993. Floral display size and pollination of the western prairie fringed orchid, *Platanthera praeclara* (Orchidaceae). Lindleyana 8: 32–38.

RALSTON, C., G. FAUSKE, M. HARRIS, & D. LENZ. 2008. First record of the spurge hawk moth (*Hyles euphorbiae*) as a pollinator of the western prairie fringed orchid. The Prairie Naturalist. In press.

RATHCKE, B.J. 2000. Hurricane causes resource and pollination limitation of fruit set in a bird-pollinated shrub. Ecology 81: 1951–1958.

ROLL, J., R.J. MITCHELL, R.J. CABIN, & D.L. MARSHALL. 1997. Reproductive success increases with local density of conspecifics in a desert mustard (*Lesquerella fendleri*). Conservation Biology 11: 738–746.

SAMSON, F.B. & F.L. KNOPF. 1994. Prairie conservation in North America. BioScience 44: 418–421.

SHEVIAK, C.J. & M.L. BOWLES. 1986. The prairie fringed orchids: a pollinator-isolated species pair. Rhodora 88: 267–290.

SMITH, W.R. 1993. Orchids of Minnesota. University of Minnesota Press, Minneapolis, Minnesota.

SOUTHWOOD, T.R.E. & P.A. HENDERSON. 2000. Ecological methods. 3rd ed. Blackwell Science, United Kingdom.

SPIGLER, R.B. & S. CHANG. 2008. Effects of plant abundance on reproductive success in the biennial *Sabatia angularis* (Gentianaceae): spatial scale matters. J. Ecology 96: 323–333.

STEPHENSON, A.G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Ann. Review Ecology and Systematics 12: 253–279.

SPSS Inc. 2001. Version 11.0.1 for Windows. Chicago, Illinois.

TUTTLE, J.P. 2007. The hawk moths of North America. The Wedge Entomological Research Foundation. Washington, D.C.

U.S. FISH AND WILDLIFE SERVICE. 1996. *Platanthera praeclara* (western prairie fringed orchid) recovery plan. U.S. Fish and Wildlife Service, Ft. Snelling, Minnesota.

WESTWOOD, A.R. & C.L. BORKOWSKY. 2004. Sphinx moth pollinators for the endangered western prairie fringed orchid, *Platanthera praeclara* in Manitoba, Canada. J. Lepid. Soc. 58: 13–20.

WHILES, M.R. & R.E. CHARLTON. 2006. The ecological significance of tallgrass prairie arthropods. Ann. Review Entomology 51: 387–412.

WILLMOTT, A.P. & A. BÚRQUEZ. 1996. The pollination of *Merremia palmeri* (Convolvulaceae): can hawk moths be trusted? American J. Botany 83: 1050–1056.

WOLKEN, P.M., C.H. SIEG, & S.E. WILLIAMS. 2001. Quantifying suitable habitat of the threatened western prairie fringed orchid. J. Range Management 54: 611–616.

ZAR, J.H. 1996. Biostatistical analysis. 3rd Edition. Prentice Hall, Upper Saddle River, New Jersey.

Received for publication 4 July 2008; revised and accepted on 17 November 2008.

Journal of the Lepidopterists' Society
63(2), 2009,118-126

ABERRANT COLOR PATTERNS IN THE *PAPILIO* AND AN UPDATE ON THE SEMI-MELANIC "*FLETCHERI*" VARIANTS, INCLUDING FEMALES (LEPIDOPTERA: PAPILIONIDAE)

J. MARK SCRIBER
Department of Entomology, Michigan State University, E. Lansing, MI 48824; research associate McGuire Center for Lepidoptera and Diversity, University of Florida, Gainesville, FL 32611-2710; email: scriber@msu.edu

HOWARD ROMACK
28 Irish Lane, Cambridge, NY 12816,

AND

MARK D. DEERING
Lepidoptera Curator, Sophia Sachs Butterfly House, 15193 Olive Blvd., Chesterfield, MO 63017

ABSTRACT. Specimens resembling the male melanic aberration called "*fletcheri*" have been reported since the 1800's, primarily from *Papilio canadensis* populations across northern USA and Canada. These records have generally exhibited similar but very distinctive wing color patterns on the upper and undersides, especially the orange and blue on the hindwings. This paper reviews the 120-year history of "*fletcheri*"-type records and presents a number of new records, including some from *P. glaucus* and one from *P. rutulus*. Other female variants are also figured and compared since "*fletcheri*" phenotypes have historically almost always been males. We report on the first known female specimen of "*fletcheri*" from Vermont and discuss another female *fletcheri* phenotype captured in eastern Washington (also in 2008). It remains unclear whether interspecific introgression between *P. canadensis*, *P. glaucus*, and *P. rutulus* plays any role in generating these rare phenotypes, but *fletcheri* specimens are all from areas near the hybrid zone. Natural environmental conditions may play some role in causing this phenotype, especially since none have been generated under lab conditions.

Additional key words: aberrant mosaics, wing color variants, bilateral gynandromorphs, *Papilio glaucus*, *P. rutulus*, semi-melanics, Nearctic, female *fletcheri*.

Melanic male aberrants of *Papilio canadensis* Rothschild and Jordan have been reported at least since the 1880's when Fletcher (1889) described a very distinctive form collected from the Collins Inlet on Georgian Bay, 18 miles east of Killarney, Ontario in Canada. The similarities in subsequent captures were noted (Table 1) and the name *Papilio turnus* ab. *fletcheri* was suggested (Kemp 1900). While apparently no new reports were made for the next 60 years, a series of at least 12 letters and papers featuring discussion of the "*fletcheri*" form appeared during the period from 1960–1983 (see Table 1; Scriber & Lintereur 1983). While most of the reported specimens are from geographic areas now known to be in the range of *P. canadensis*, there are some putative "*fletcheri*" phenotypes from *P. glaucus* (Table 1). There has apparently been no successful rearing of offspring from a "*fletcheri*" parent (of either sex) and we still lack genetic studies of this form. Here we report our attempts to obtain offspring from "*fletcheri*" male parent and describe nine new male "*fletcheri*" (including *P. glaucus* and *P. rutulus* population sources) and female aberrants that could represent a form of "*fletcheri*".

METHODS AND RESULTS

New specimens of "*fletcheri*" from three different *Papilio* species. We report the capture and present figures of two "*fletcheri*" from northern Wisconsin (Sawyer and Oconto Counties; Figs. 1–3) and two from northern Michigan (Presque Isle and Cheboygan Counties, Figs. 4–5). The male from Cheboygan County (Fig. 5) was hand-paired to virgin females upon return to the lab in an attempt to see if this trait was dominant and whether it would occur in daughters as well as sons. However, we were unsuccessful at obtaining offspring from either pairing. On 31 May 1991 we hand-paired this male to a virgin *P. canadensis* female. While copulation lasted 49 minutes, no eggs were laid. A second pairing of this male was made to a lab-reared virgin *P. glaucus* female. Copulation lasted 51 minutes and eggs were laid on tulip tree (*Liriodendron tulipifera* L., Magnoliaceae), white ash (*Fraxinus americana* L., Oleaceae) sassafras (*Sassafras albidum* (Nutt.) Nees, Lauraceae) and black cherry (*Prunus serotina* Ehrh., Rosaceae), but none were fertile.

Field collections in eastern New York state and southwestern Vermont yielded five male "*fletcheri*"

types (during the period 1982–1999; Figs. 6–10; Table 1). These Vermont specimens all appear to be from areas that historically were *P. canadensis* while the New York specimen (Fig. 10) looks much more like *P. glaucus*, based on the inner black band width of the hindwing cell (Luebke *et al.* 1988; Scriber 2002). Cambridge, New York is a site that we have observed for two decades and recently, during the last two to three years, a second flight of *P. glaucus* has been observed. The Vermont populations of *P. canadensis* in adjacent southwest Vermont (Bennington County) have shown some evidence of extensive genetic introgression from *P. glaucus*, possibly from longer growing seasons (degree day thermal accumulations) during the mid-1990s (Scriber & Gage 1995; Scriber *et al.* 2008). This delayed "false second generation" flight in mid-July is much more hybrid-like than the May–June individuals and may represent the prototype (incipient species) or early stage of the mountain swallowtail, *P. appalachiensis* (Pavulaan & Wright 2002), which appears to be a recombinant (homoploid) hybrid species, unique genetically but sharing a delayed flight and many hybrid-like traits (Scriber & Ording 2005; Scriber *et al.* 2008). The late-June specimen (Fig. 10) appears to reflect these intermediate wing traits, while the early June and May specimens from the same Battenkill River Valley populations (Fig. 6–9; Table 1) do not.

Other specimens with "*fletcheri*" wings. A "*fletcheri*" type *P. rutulus* was collected in Lincoln County, Wyoming on 28 June 1973 (Fig. 11). Once again, we are not certain about the degree of introgression (if any) from other species such as *P. canadensis* and *P. glaucus*, although *P. eurymedon* and *P. multicaudatus* (see Scriber *et al.* 1990, 1995) do not appear to be involved here (see also field collected interspecific hybrids described in Guppy & Shepard 2001).

A *P. glaucus* "*fletcheri*" type was collected in Frederick County, MD on 29 July 1978 by Joseph Zeligs (Table 1; Fig. 12). It is very much *glaucus*-like in wing morphometrics and near to the *glaucus-canadensis* hybrid zone further inland in the Pennsylvania/West Virginia Appalachian Mountains (Scriber 1990).

In 2008, before acceptance/revision of this manuscript, we were fortunate in obtaining a female "*fletcheri*" phenotype from Bennington County, Vermont (captured by H. R. 27 May 2008; Fig. 21). Also, a female *fletcheri* (possibly *P. rutulus*) from eastern Washington, near the Canadian border, was figured in a web site (dorsal view: http://www.insectnet.com/dcforum/User_files/485349cd202d92a7.jpg; ventral view: http://www.insectnet.com/dcforum/User_files/485349dc48c9c1e6.jpg). This Washington state specimen was also captured in 2008 on 1 June, by Robert Goodmiller, and this female looks almost identical to the one we figure here. These two specimens are the only clear examples of female "*fletcheri*" phenotypes.

DISCUSSION

These melanic male "*fletcheri*" types (clearly distinguishable from color mosaics and gynandromorphs) are apparently inherited independently of the (Y-linked, X-modified) melanic polymorphism that characterizes females of the *Papilio glaucus* and *Papilio alexiares* species (Clarke & Sheppard 1962; Scriber *et al.* 1996). In rearing more than 15,000 different families (offspring of a single female) of the *P. glaucus* group (producing approximately 80,000–100,000 adults) we have never seen a "*fletcheri*" type emerge. We report here that the "*fletcheri*" type is found in the natural populations of the western tiger swallowtail, *P. rutulus*, from Wyoming, as well as New England, Michigan, Wisconsin and Canada populations of *P. canadensis* (Figs. 1 and 2). Before the revision of this paper in 2008, we had not confirmed that female "*fletcheri*" exist, but some literature records suggest it is likely (Table 1; Brewer 1977; Drees 1977). However, from the photo and discussion, the individual depicted in Brewer (1977) from Virginia may be a semi-melanic gynandromorph (not a pure female). The semi-melanic female reported by Miller (1990; Table 1) may also represent a different "dark cells" type (Scriber & Evans 1988a and see discussion below; Fig. 13a). The female melanic reported by Drees (1978) was not figured. Therefore, we report here, officially, that "*fletcheri*" coloration does exist in females.

Another superficially similar dorsal wing melanism, called "dark cells", reported only from females of *P. glaucus* occurs as black blotches throughout the dorsal surface of forewings, especially distally (Figs. 13). This melanic aberration is heritable, appearing in 29 of 38 daughters of two sibling pairs from a "dark cell" type mother (Scriber & Evans 1988b).

Melanic wing patterns (bilaterally symmetrical) in female tiger swallowtails from the Great Lakes hybrid zone of *P. canadensis* and *P. glaucus* (Scriber 1996a) have also been described (Scriber 1990). These distinctive patterns have the black band virtually completely filling the anal cell of the hindwing, but otherwise appear to have near-normal, tiger-striped patterns with "vein smearing" of dark scales. Some additional suffusion of dark scales appears to widen the black tiger stripes. Both specimens described came from different mothers with normal wing coloration

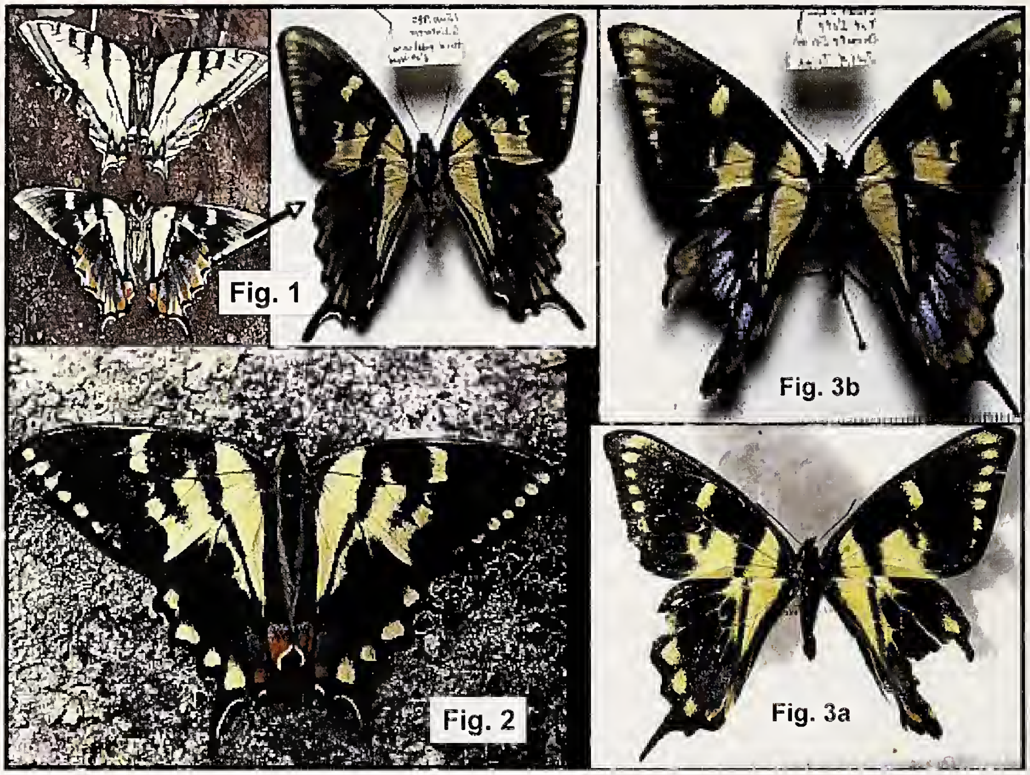


FIG. 1-3. **(1)** Ventral view of male *"fletcheri"* phenotype *P. canadensis* from Sawyer Co., WI near Pigeon Lake, shown with a normal male (Greg Lintereur captured 2 June 1980). **(2)** Dorsal view of *"fletcheri"* speeimen (of Fig. 1). **(3a,b)** Dorsal (a) and ventral (b) view of male *"fletcheri"* phenotype *P. canadensis* (Joel Triek captured 6 June 1980 in Oconto, Co., WI).

FIG. 4-5. **(4a,b)** Dorsal/ventral view of male "fletcheri" from Presque Isle Co., MI (27 May 1991, Jim Keller). **(5a,b)**. Dorsal/ventral view of male *"fletcheri"* from Cheboygan Co., MI (June 1992, J. M. Scriber).

Fig. 6 a,b Fig 7 a,b Fig. 8 a,b

FIG. 6–8. Dorsal and ventral views of *"fletcheri"* types collected by H. Romack, all in southwestern Vermont (Bennington Co.). **(6)** 26 May 1982 male *P. canadensis*. **(7)** 12 June 1983 male *canadensis*. **(8)** 6 May 1995 male canadensis.

Fig. 9 a,b Fig. 10 a,b Fig. 11 a,b

FIG. 9–10. Dorsal and ventral views of "fletcheri" types collected by H. Romack, all in southwestern Vermont (Bennington Co.). **(9)** 6 June 1995 male canadensis. **(10)** A male *P. canadensis "fletcheri"* from Washington Co. (26 June 1999, Cambridge) NY. **(11)** A male *P. rutulus "fletcheri"* from Lincoln Co., Wyoming 28 June 1983.

patterns (Fig. 14; Scriber 1990). Here we figure two recent specimens from northern Michigan that appear to have similar patterns, again only seen in the females, not in their male siblings.

Another melanic aberration found, to our knowledge, only in males has the inner third of the wings (dorsal and ventral, forewings and hindwings) melanic, with a light to heavy (solid) "dusted" appearance (Fig. 15; Scriber & Evans 1987). Except that the aberration occurred in males, it might be considered as a variant on the continuum of "intermediate" between the female polymorphism of normal yellow tiger striped or dark form. Such completely dusted-looking intermediates (Figs. 16 & 17) are common in females (usually only in offspring from dark form mothers; Edwards 1884; Scriber *et al.* 1996) and may be induced by rearing at higher temperatures. Similar melanism on the proximal 1/3 of wings of females has also been described (Clark 1932; Clark & Clark 1951) and may in fact represent incomplete expression of the Y-linked melanic female form (due to only partial suppression by an X-factor; Scriber *et al.* 1996) or due to environmental factors (e.g. high temperatures; Ritland 1986). It is interesting that the males carrying this inner wing melanism trait were also suspected to be carriers of the Y-linked melanism trait previously believed found only in females (Scriber & Evans 1987).

Variations of melanism (dark cells, "sooty", intermediates, and semi-melanics), as shown in Figs 13–17, may be the result of multiple enzyme activities which regulate underlying synthetic pathways for melanization via a single Y(=W)-linked (female) genetic factor (Clark & Sheppard 1962; Scriber *et al.* 1996; Koch *et al.* 2000; Ffrench-Constant & Koch 2003). Other hypotheses, such as broadening of the dark pattern elements, have been proposed as a model of melanism in *P. glaucus* (Nijout 1991). However, these recent molecular studies of the biochemistry of the enzymes dopa decarboxylase show that it affects both of the two major scale color pigments, papiliochrome (yellow) and melanin (black) and that the melanization occurs later in the formerly yellow area. The single major sex-linked gene (the Y-linked black or b+ gene) and a modifying gene (the X-linked suppressor, s+; Scriber *et al.* 1996), that interact in the hybrid zone with suppression of the dark potential, are compatible with

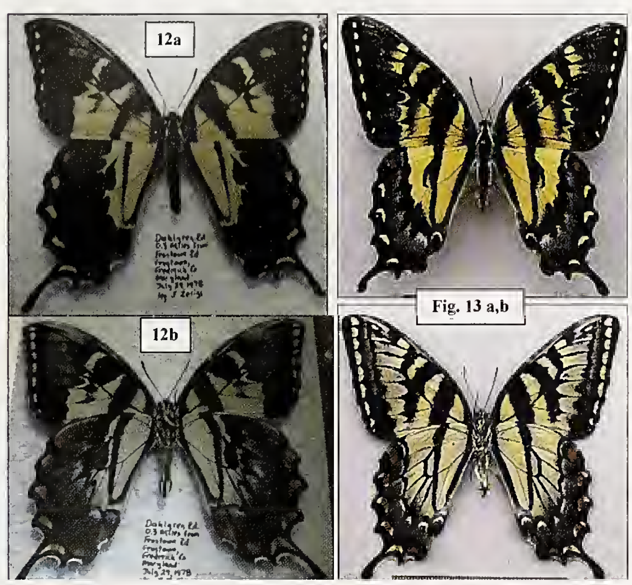


FIG. 12–13. **(12)** Dorsal and ventral views of *"fletcheri"* type male *Papilio glaucus* from Frederick Co. Maryland (captured 29 July 1978 by J. Zeligs, pers. comm. to JMS). **(13)** Dorsal/ventral views of the "dark cells" female expressed trait (Scriber & Evans 1988a).

FIG. 14. **(14)** Dorsal **(a)**/ventral **(b)** views of 2 "vein-smeared" females emerged in August 1997 reared from 2 mothers caught in Chippewa Co., MI. These phenotypes have been reared from four different females of Chippewa Co. (family #12229, 12230, 12235, 12236) and from wild female from Cheboygan Co. **(15)** Dorsal/ventral view of male melanic with dusted inner wings only (Scriber & Evans 1987).

FIGS 16 & 17. Dorsal/ventral views of two sibling females showing "intermediate" dark morph coloration family #1396 of a Texas dark female x *P. canadensis* male from Marquette Co., Wisconsin, in the hybrid zone (Scriber et al. 1996).

the biochemical results described by Koch *et al.* (1998). However, except for the tendency to produce intermediate lightly dusted dark females at warmer temperatures (for females with the b+ gene; Ritland 1986), the reasons for aberrant melanic patterns remain basically unknown, although they appear genetically based since they are passed to some offspring (sometimes including males; Scriber & Evans 1987, 1988a). For example, odd-segregating dark daughters (2/3 of the individuals) in two different families (one *P. canadensis* female, and the other a yellow *P. glaucus* female) that were sired by a single "sooty" male (as Fig. 15) cannot be explained by any genetic patterns known to date (Scriber *et al.* 1996). Normally only the heterogametic lepidopteran females [XY (=ZW)] would have the Y-linked b+ gene for black. However, the remote possibility exists that a piece of the Y-chromosome (with the b+ black gene) broke off and translocated to another autosome without losing its expression potential, explaining the odd results of Scriber & Evans (1987). A similar case of chromosomal translocation was described for moths by Marec *et al.* (2001).

In contrast, the "*fletcheri*", believed to be a stable low-level polymorphism of *P. canadensis*, has now been

TABLE 1. Literature records of the *Papilio* semi-melanic aberration putatively of the type called "*fletcheri*".

Collecting Location	Date/Year	Collector	Reference
Collins Inlet on Georgian Bay, 18 miles east of Killarney,ONT	(July 1888) (male,*P. canadensis*)	Robert Mackenzie	Fletcher 1889
Orillia, Ontario	(male, *P.c.*)	C.E. Grant	Grant 1896
Elizabeth, NJ	July 1899 (male, ?)	A. Ronke	Kemp 1900
Forest County, WI	16 June 1958 (male, *P.c.*)	Louis Allen	Ebner 1960
Gorge Creek/Hwy #11, north of Nipigon, Ontario	27 June 1961 (male, *P.c.*)	E.M.S. (?)	Sicher 1962
Brown's Mill, Fairfax Couty, VA	August 1976 (female P. *glaucus*, gynandromorph?)	Richard H. Smith	Brewer 1977
Penland, NC	August 1975 (male, *P. glaucus*)	R. Peter Rosier	Rosier 1977
Source ?	18 ?? (*P. glaucus*)	Herman F. Strecker	Walsten 1977
Brighton, MI	May 1977 (sex?, *P.g./P.c.*)	Marc W. Grocoff	Grocoff 1977
Salem, VA	August 1975 (sex?/*P. glaucus*)	Fred Eichleman	Eichleman 1977
Clothier, WV	24 August 1972 (female, *P. glaucus*)	Tom Allen	Drees 1978
Markham, Ontario, Canada	June 1978 (sex?/*P.c.*)	John Johnstone	Johnstone 1978
Great Smoky Mountains Little Pigeon River, Sevier Co. TN	2 August 1979 (*P.g./P.c.?*)	Mecky Furr	Brewer 1980
Source?	Reports seeing *fletcheri* type in *P. eurymedon* but not *rutulus*	Art Shapiro	Shapiro 1981
Frederick County, MD	24 July 1978 (male, *P.g.*)	Joseph D. Zeligs	(pers. corresp.)(Fig. 12)
Pigeon Lake, WI, (Sawyer County, WI)	2 June 1980 (male *P.c.*)	Greg Lintereur	Scriber and Lintereur 1983, (Fig. 1)
Green Bay, Oconto County, WI	6 June 1980 (male *P.c.*)	Joel Trick	Scriber and Lintereur 1983 (Fig. 4)
Bethel Park, PA	Summer 1990 (female *P. glaucus*)	Monica Miller	Miller 1990
Presque Isle County, MI	27 May 1991 (male *P.c.*)	Jim Keller	Scriber *et al.* 1995, (Fig. 5)
Cheboygan County, MI	June 1992 (male *P.c.*)	Mark Scriber	Scriber *et al.* 1995
Southwest VT	26 May 1982 (male *P.c.*)	Howard Romack	Fig. 6
Southwest VT	12 June 1983 (male *P.c.*)	Howard Romack	Fig. 7
Southwest VT	6 May 1995 (male *P.c.*)	Howard Romack	Fig. 8
Southwest VT	6 June 1995 (male *P.c.*)	Howard Romack	Fig. 9
Cambridge, NY, (Washington County)	26 June 1999 (male *P.c.*)	Howard Romack	Fig. 10
Lincoln County, WY	28 June 1973 (male *P. rutulus*)	P. Grey	Fig. 11
Gunnison Co. Colorado	2004 2 male *P. rutulus*	Matthew Garhart	(Clark 2006)
Bennington Co. Vermont	2008 female	Howard Romack	Fig. 13
Eastern Washington	2008 female	Robert Goodmiller	http://www.insectnet.com/dcforum/User_files/485349dc48c9c1e6.jpg

Fig. 18 a,b Fig. 19 a,b Fig. 20

FIGS. 18-20. Dorsal/ventral view of aberrant *P. canadensis* female from Ontario, Canada (5 June 1995) with submarginal wing cell coloration elongated. **(19).** *P. troilus* from Glenns Falls (8 July 1987; Warren Co., NY); submarginal wing cell coloration elongated (as with Fig. 18). **(20).** Potential *"fletcheri"* type (courtesy of David and Marc Perlman).

shown to also occur in *P. glaucus* and *P. rutulus*. In addition to our observation, two male specimens of *"fletcheri"*-like individuals were found in *P. rutulus* from Gunnison County, Colorado by Mathew Garhart in 2004 (Clark 2006). This suggests the possibility of a common evolutionary origin of this polymorphic development color pathway in wings many millions of years ago in a common ancestor of the tiger swallowtail butterflies. Alternatively, it may reflect recent or historical hybridization of *P. canadensis* with *P. glaucus* and *P. rutulus* (Guppy & Shepard, 2001; but see Sperling 1993).

We are not sure if interspecific hybridization between *P. glaucus* and *P. canadensis* played any role in the enhanced rate of expression of the *"fletcheri"* type wing patterns at the Battenkill River Valley between Vermont and New York (or elsewhere). However, the *"fletcheri"* specimen from Frederick Co., MD (Fig. 12; Zelig, pers comm.) was captured at the end of July (a late flight) and may represent a specimen of *P. appalachiensis* (which may be a hybrid species and is known to fly in that county of Maryland; Pavulaan & Wright 2002). This raises the possibility that *glaucus-canadensis* hybridization may have been involved (Scriber *et al.* 2008) as may be the case in the late June specimen (Fig. 10) from New York, near Vermont. Similarly, the area of Washington that produced a female *"fletcheri"* in 2008 is also near areas with suspected hybrids between *P. canadensis* and *P. rutulus* (Guppy & Shepard 2001; but see Sperling 1993).

While we are not really certain that hybrid introgression has anything directly to do with causing the *"fletcheri"* phenotype, it is still worthwhile pointing out the fact that all examples of this phenotype are in areas where hybridization is known to occur. Natural environmental conditions may play some major role in causing this phenotype, especially since none have been

FIG. 21. Female fletcheri **a)** dorsal **b)** ventral; Vermont, Bennington County, Kelly Stand Road, 27 May 2008 (HR).

generated under controlled lab conditions for many thousands of individuals.

Other non-*fletcheri* type aberrants. We also have observed some additional aberrant color patterns in specimens from Canada, New York, and Vermont. The submarginal cell color elongation in *P. canadensis* (Fig. 18) and *P. troilus* (Fig. 19) look similar to the *P. troilus* aberration called "*radiatus*" by Clark (1932) (see also *P. troilus* specimen collected by Raymond Thomas 12 April 2006 from Fremont, Missouri; Clark 2006). Another odd individual image was sent by David Perlman (Fig. 20), which may or may not be a "*fletcheri*".

ACKNOWLEDGEMENTS

This research was supported in part by the Michigan State Agricultural Experiment Station (MAES Project #1644) and the National Science Foundation (DEB 9981608 and DEB 0716683). We thank Matt Ayres, Janice Bossart, Jessica Deering, Mark Evans, Jim Keller, Robert Lederhouse and James Nitao for their assistance in the field and/or laboratory. Thanks are extended to Austin Platt, Matthew Aardema, and Rodrigo Mercader for their reviews and to David and Marc Perlman for supplying pictures of their specimens. We were not able to secure permission from Robert Goodmiller for including his photos of the female *fletcheri* aberrant from Washington. We thank Fred Bower and an anonymous reviewer for helpful comments on the manuscript.

LITERATURE CITED

BREWER, J. 1977. The darkling butterflies. News. Lepid. Soc. Mar./Apr. pp. 16–17.

_____. 1980. Message from Ripples editor. News Lepid. Soc. May/June no. 3, p. 35.

CLARK, A. H. 1932. The butterflies of the District of Columbia and vicinity. Smithsonian Inst.USMN Bull. 157: 172–199.

CLARK. D. 2006. From the editor's desk. News Lepid. Soc. 48: 92

CLARKE, C.A. & P. M. SHEPPARD. 1962. The genetics of the mimetic butterfly *Papilio glaucus*. Ecology 43: 159–161.

DREES, B. M. 1978. Letter to the editor; Ripples. News of the Lepidopterists' Society Jan./Feb. no. 1, p. 3.

EBNER, J. A. 1960. Striking melanic male of *Papilio glaucus*. J. Lepid. Soc. 14: 157–158.

EDWARDS, W. H. 1884. The butterflies of North America (2nd series). Volume II. Houghton Mifflin, Boston.

EICHLEMAN, F. 1977. Letter to the editor. News Lepid. Soc. Sept./Oct., p. 7.

FFRENCH-CONSTANT, R. H. & P. B KOCH. 2003. Mimicry and melanism in swallowtail butterflies: toward a molecular understanding. Pp. 259–280. *In* C. L. Boggs, W. B Watt, & P.R. Ehrlich (eds.), Butterflies: ecology and evolution taking flight. Univ. Chicago Press, Chicago.

FLETCHER, J. 1889. The tiger-swallowtail (*Papilio turnus*, L.). Canad. Entomol. 21: 201–204.

GRANT, C. E. 1896. Butterflies taken at Orillia, Ontario. Canad. Entomol. 28: 271–274.

GROCOFF, M. W. 1977. Letter to the editor; Ripples. News Lepid. Soc. Sept./Oct., p. 7.

GUPPY, C. S. & J. H. SHEPARD. 2001. Butterflies of British Columbia. University of British Columbia Press, Vancouver, BC.

Johnstone, J. 1978. Letter to the editor, Ripples. News Lepid. Soc. Nov./Dec. no. 6, p. 9.

KEMP, S. T. 1900. Notes and news. Entomol. News. (May) pp. 481–482.

KOCH, P. B., B. BEHNECKE, M. WEIGMANN-LENZ, & R. H. FFRENCH-CONSTANT. 2000. Insect pigmentation: activities of B- alanyldopamine synthetase in wing color patterns of wild type and melanic mutant swallowtail butterfly *Papilio glaucus*. Pigment Cell Res. 13: 54–58.

_____, D. N. KEYS, T. ROCHELEAU, K. ARONSTEIN, M. BLACKBURN, S. B. CARROLL, & R. H. FFRENCH-CONSTANT. 1998. Regulation of Dopa decarboxylase expression during color pattern formation in wild-type and melanic tiger swallowtails. Development 125: 2303–2313.

LEUBKE, H. J., J. M. SCRIBER & B. S. YANDELL. 1988. Use of multivariate discriminant analysis of male wing morphometrics to delineate the Wisconsin hybrid zone for *Papilio glaucus* and *P.g. canadensis*. Amer. Midl. Natur. 119: 366–379.

MAREC, F., A. TOTHOVA, K. SAHARA, & W. TRAUT. 2001. Meiotic pairing of sex chromosome fragments and its relation to atypical transmission of a sex-linked marker in *Ephestia kuehniella* (Insecta: Lepidoptera). Heredity 87: 659–671.

MILLER, M. 1990. From the editor's desk. Lepid. News. p. 4.

NIJOUT, H. F. 1991. The development and evolution of butterfly wing patterns. Smithsonian Institution Press, Washington, DC.

PAVULAAN H. & D. M. WRIGHT. 2002. *Pterourus appalachiensis* (Papilionidae: Papilioninae), a new swallowtail butterfly from the Appalachian region of the United States. Taxonom. Report, 3: 1–20.

RITLAND, D. B. 1986. The effect of temperature on the expression of the dark morph phenotype in female *Papilio glaucus* (*Papilion*idae). J. Res. Lepid. 25: 179–187.

ROZIER, R. P. 1977. Letter to the editor; Ripples. News Lepid. Soc. July/Aug. no. 4, p. 2.

SCRIBER, J. M. 1990. Two new aberrant forms of tiger swallowtail butterfly *Papilio glaucus* from the Great Lakes hybrid/transition zone. Great Lakes Entomol. 23: 121–126.

_____. 1996. Tiger tales: Natural history of native North American swallowtails. Amer. Entomol., 42: 19–32.

_____. 2002. The evolution of insect-plant relationships; Chemical constraints, coadaptation and concordance of insect/plant traits. Ent. exp. et appl. 104: 217–235.

_____, R. DOWELL, R. C. LEDERHOUSE, & R. H. HAGEN. 1990. Female color and sex ratio in hybrids between *Papilio glaucus* and *P. eurymedon*, *P. rutulus* and *P. multicaudatus* (*Papilio*nidae). J. Lepid. Soc., 44: 229–244.

_____ & M. H. EVANS. 1987. An exceptional case of paternal transmission of the dark form female trait in the tiger swallowtail butterfly, *Papilio glaucus* (*Papilio*nidae: Lepidoptera). J. Res. Lepid., 26: 32–38.

_____ & _____. 1988a. A new heritable color aberration in the tiger swallowtail butterfly, *Papilio glaucus* (Papilionidae: Lepidoptera). J. Res. Lepid. 26: 32–38.

_____ & _____. 1988b. Bilateral gynandromorphs, sexual and/or color mosaics in the tiger swallowtail, *Papilio glaucus* (Papilionidae: Lepidoptera) J. Res. Lepid., 26: 39–57.

_____, M. H. EVANS, & D. RITLAND. 1987. Hybridization as a causal mechanism of mixed color broods and unusual morphs of female offspring in the eastern tiger swallowtail butterflies, *Papilio glaucus*. Pp. 119–134. *In* M. Huettel (ed.), Evolutionary genetics of invertebrate behavior. Univ. of Florida, Gainesville, FL.

_____ & S. GAGE. 1995. Pollution and global climate change: Plant ecotones, butterfly hybrid zones, and biodiversity. Pp. 319–344. *In* J. M. Scriber, Y. Tsubaki & R. C. Lederhouse (eds.), The swallowtail butterflies: their ecology and evolutionary biology. Scientific Publishers, Inc., Gainesville, FL.

_____ & R. H. HAGEN. 1990. Bilateral differentiation of color and morphology in the larval and pupal stages of a tiger swallowtail, *Papilio glaucus*. Great Lakes Entomol. 23: 139–143.

_____, R. H. HAGEN, & R. C. LEDERHOUSE. 1996. Genetics of mimicry in the tiger swallowtail butterflies, *Papilio glaucus* and *P. canadensis* (Lepidoptera: Papilionidae). Evolution 50: 222–236.

_____, R. C. LEDERHOUSE, & R. DOWELL. 1995. Hybridization studies with North American swallowtails. Pp. 269–282. *In* J. M. Scriber, Y. Tsubaki, & R. C. Lederhouse (eds.), The swallowtail butterflies: their ecology and evolutionary biology. Scientific Pub-

lishers, Inc., Gainesville, FL.
_____ & G. Lintereur. 1983. A melanic male aberration of *Papilio glaucus canadensis* from northern Wisconsin. J. Res. Lepid. 21: 199–201.
_____ & G. Ording. 2005. Ecological speciation without host plant specialization: possible origins of a recently described cryptic *Papilio* species (Lepidoptera: Papilionidae) Ent. Exp. et Appl. 115: 247–263.
_____, G. J. Ording, & R. J. Mercader. 2008. Hybrid introgression and parapatric speciation in a hybrid zone. Pp. 69–87. *In* K. Tilmon (ed.), Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects. Univ. California Press.
SHAPIRO, A. M. 1981. Letter to the editor; Ripples. News Lepid. Soc. Jan./Feb. no. 1, p. 5.
SICHER, E. 1962. A mosaic melanic male of *Papilio glaucus*. J. Lepid. Soc. 16: 98.
SPERLING, F. A. S. 1993. Mitochondrial DNA variation and Haldane's rule in the *Papilio glaucus* and *P. troilus* species groups. Heredity 71: 227–233.
WALSTEN, D. M. 1977. To the editor; Ripples. News Lepid. Soc. Sept./Oct. no. 5, p. 6.

Received for publication on 26 February 2008; revised and accepted on 3 July 2008.

Journal of the Lepidopterists' Society
63(2), 2008, 127

NOTES ON THE BIOLOGY OF THE GULF FRITILLARY, *AGRAULIS VANILLAE* (LEPIDOPTERA: NYMPHALIDAE), IN NORTH-CENTRAL FLORIDA

Additional key words: *Lespesia aletiae*, *Hyphantrophaga virilis*, Diptera, Tachinidae, behavior, larvae, parasitism, parasitoid, diapause, migration, host plant, *Passiflora*.

Agraulis vanillae L. is one of the most common butterflies in Gainesville, north-central Florida, where it flies throughout the year (G.T. Austin, pers. com.; Kons & Borth 2006). Its larvae can be found on native *Passiflora incarnata* L. and on other (frequently exotic) passion vines in the area. Larvae can be found through late fall, until the first hard freeze (usually in December) kills the above-ground portion of the passion-vine.

Scott (1979) suggested that *A. vanillae* is not known to diapause, and listed as its winter stages larva, pupa, and adult. However this cannot be true for the species' entire distribution area (North Carolina to Patagonia). *A. vanillae* is migratory, moving southward in the fall and northward in the spring (Walker 2001). The question remains, do any individuals overwinter locally as larvae and pupae, and if so, is either stage capable of diapause? Observations reported here indicate that, in north-central Florida, *A. vanillae* can apparently diapause not only as pupae but as larvae.

In 2007–2008, I observed hundreds of larvae (abundant in October–November) pupating on the vegetation surrounding the host plants. Some pupae remained dormant until spring, while some were observed to emerge in January even after hard freezes. Many larvae (mostly fifth-instar) that were unable to complete development prior to freezing of the host plant were not killed by the freeze, though they remained motionless or were even knocked down to the ground by the cold temperatures and wind. The lowest monthly average temperature in the area is relatively high: 66.2°F in January (according to National Climatic Data Center). When the temperatures rose above 60°F, larvae dispersed away from the host plant, but could be found occasionally on surrounding vegetation months later. In March, when the first shoots of *P. incarnata* sprouted, I found mature *A. vanillae* larvae on them almost immediately, which indicates that they survived without food source for a period of four months in what seems to be a semi-active diapause.

An interesting behavior was exhibited by mature *A. vanillae* larvae coming out of diapause and beginning to feed on fresh shoots of *Passiflora caerulea* L. This passion vine exuded abundant sweet-tasting (pers. obs.) sap, not only from the nectaries, but also from the leaf veins where the latter were cut by larval feeding. Larvae appeared to be deliberately drinking this sap by selecting individual droplets with their mandibles and sucking the droplets in. Perhaps this behavior is induced by dehydration resulting from the four-month-long interruption in feeding during diapause.

From 20 last-instar larvae collected in late November and allowed to pupate in captivity, 90% were found to be parasitized. The tachinid flies that emerged from the pupae belonged to three species: *Lespesia aletiae* (Riley), *Hyphantrophaga virilis* (Aldrich & Webber), and a yet-undetermined *Hyphantrophaga* species (voucher specimens were deposited in the Canadian National Collection of Insects). Arnaud (1969) found a tachinid, *Compsilura concinnata* (Meigen) (introduced from Europe), in 2% (N=50) of field-collected larvae in northern California, and Castellar & Figuero (1969) noted that *A. vanillae* is parasitized by unidentified Tachinidae in Brazil.

Acknowledgements

I would like to thank James E. O'Hara and D. Monty Wood for identifying the flies and George T. Austin for proofreading this note and for sharing his records of *A. vanillae* seasonal presence in Florida.

Literature Cited

Arnaud, P.H., Jr. 1969. *Compsilura concinnata* (Meigen) (Diptera: Tachinidae) reared from *Agraulis vanillae incarnata* (Riley) (Lepidoptera: Nymphalidae) at San Leandro, California. Pan-Pacific Entomol. 45(1): 77.

Castellar, P.N., & E.A. Figuero. 1969. Study of the bionomics of two Lepidoptera : *Agraulis vanillae* (Linn.) and *Mechanitis veritabilis* (Butler) on passion fruit (*Passiflora edulis* var. *flavicarpa*, D). Acta Agron. Palmira 19(1): 17-30.

Kons, H.L., Jr., and R.J. Borth. 2006. Contributions to a study of the diversity, distribution, habitat association, and phenology of the Lepidoptera of Northern Florida. North American J. Lepid. Biodiv. 1: 1-231. [on file at the McGuire Center]

Scott, J.A. 1979. Hibernal diapause of North American Papilionoidea and Hesperioidea. J. Res. Lepid. 18(3): 171-200.

Walker, T.J. 2001. Butterfly migrations in Florida: Seasonal patterns and long-term changes. Envir. Entomol. 30(6): 1052-1060.

Andrei Sourakov, *McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA; email: asourakov@flmnh.ufl.edu.*

Received for publication 15 May 2008; revised and accepted 17 November 2008.

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, General Notes, Technical Comments, Book Reviews, Obituaries, Feature Photographs, and Cover Illustrations. Obituaries must be authorized by the president of the society. Requirements for Feature Photographs and Cover Illustrations are stated in Volume 44(2):111 and on the Society's web site at http://www.lepsoc.org/.

Send *Journal* submissions electronically to: scholtensb@cofc.edu or to the editor at the above address. Contributors should feel free to recommend one or two reviewers upon submission of their manuscript. Send requests to review books for the *Journal* and book review manuscripts to Phil DeVries at the above address (or electronically to: pdevries@uno.edu). Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, Dale Clark, 1732 South Hampton Rd, Glenn Heights, TX 75154-8530. ***Before submitting manuscripts or electronic files***, consult instructions on the Society's web site at http://www.lepsoc.org/.

Although we prefer electronic submissions, authors may submit hard copy if they are unable to send material electronically. Submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white letter-sized paper. Prepare manuscript according to the following instructions, and submit them flat, not folded. Submit original illustrations only *after* the manuscript has been revised and accepted. Authors should provide an electronic copy of the *final accepted* manuscript in a standard PC or Macintosh-based word processing format.

Abstract: Include an informative abstract for Articles, Profiles, and Technical Comments.

Additional key words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Write with precision, clarity and economy, and use the active voice and the first person whenever appropriate. Make title explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Use metric units for measurements, and a 24-h clock (0930 h, not 9:30 AM) to express time. Underline only where *italics* are intended.

Literature cited: References to Articles, Profiles, General Notes, and Technical Comments should be given as Sheppard (1959) or (Sheppard 1959, 1961a,b) and listed alphabetically under the heading Literature Cited, in plain text (do not capitalize author names) and without underlining as follows:

Sheppard, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.

—— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

Illustrations: Again, electronic submissions are preferred. Initial submissions may be low-resolution *.jpg format, but final illustrations should be *.tif format at a resolution of at least 120 pixels per cm saved to a CD. Illustrate only half of symmetrical objects such as adults with wings spread, unless whole illustration is crucial. Bear in mind that your illustrations will be reduced to fit a *Journal* page (plan to make lettering sufficiently large) and that the figure legend will appear at the bottom of the page (*Journal* page: 16.5 cm width, 22.5 cm height). One-column illustrations should be at least 800 pixels wide; two-column illustrations should be 1700 pixels wide. Illustrations larger than letter-size are not acceptable and should be reduced photographically to that size or smaller. Figures, both line drawings and photographs, should be numbered consecutively in Arabic numerals; do not use "plate." Type figure legends double-spaced, *on a separate sheet* (not attached to the illustrations), headed Explanation of Figures. Use a separate paragraph for each legend. Color illustrations are encouraged; contact editor or consult our web site for submission requirements and cost.

Tables: Number tables consecutively in Arabic numerals. Label them in plain text (e.g., Table 1.) and use a concise and informative heading. Type each table on a separate sheet and place after the Literature Cited section, with the approximate desired position indicated in the text. Avoid vertical lines and vertical writing. Submit tables as Microsoft Excel or Word documents, or as TIF image files at 300 ppi.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting the identity of organisms can be found. Kinds of reports that require vouchering include descriptions of new taxa, life histories, host associations, immature morphology, and some experimental studies.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes will be charged to authors at the rate of $3.00 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are $50 per *Journal* page. For authors without institutional support, page charges are $25 per *Journal* page. For authors who are not members of the Society, page charges are $75 per *Journal* page. Authors unable to pay page charges for any reason should apply to the editor at the time of submission for a reduced rate. Authors of Book Reviews and Obituaries are exempt from page charges.

Correspondence: Address all matters relating to the *Journal* to the editor. Address book reviews directly to the book review editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

∞ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanance of Paper).